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Forest Regeneration on the Osa Peninsula, Costa Rica

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Contents

Thesis Abstract

Woody species diversity of secondary forest has the potential to converge with that found in old growth forest. This study is the first to examine multiple aspects of species and reproductive trait diversity, and their relationship to each other, across a successional chronosequence encompassing recently abandoned pasture, older second growth, and old growth forest. We focused on dispersal mechanism, pollinator, diaspore length, and fruit length as key reproductive traits. Species richness and species diversity increases with increasing age of forest. Diaspore size and diversity as well as fruit size generally increased with increasing age of forest, but fruit size diversity did not significantly change with increasing age of forest. Abundance of animal-dispersed species increased whereas wind-dispersed species decreased in abundance over succession. Insect-pollinated individuals were most abundant, especially in early and mid-second growth forests, whereas wind-pollinated individuals were more abundant in late second-growth forests and even more abundant in old growth forests. Diaspore diversity, pollination diversity, and reproductive trait richness were significantly correlated with species richness, but other measures of reproductive trait diversity were not. Our results suggest that different community assembly processes involve different reproductive traits, and that secondary forest plots are on a trajectory to recover levels of diversity found in old growth forest.

Recovery of anthropogenically disturbed forest can also be affected by remnant trees, left when tropical forests are cleared for agriculture or grazing. These old growth trees act as nuclei of forest regeneration following field abandonment. This study is among the first to investigate the effects of remnant trees on nearby forest structure and biodiversity, 20-30 years post-abandonment. Regeneration of woody species $\geq$ 1 cm or 5 cm diameter at breast height (dbh) beneath remnant trees does not significantly differ in density or basal area. Species richness is

higher around remnant trees than around reference trees. The species composition around remnant trees is significantly different from that around reference trees and more closely resembles that of nearby old growth forest. A multinomial classification method to categorize species as old growth specialists, second growth specialists, or generalists used in the chronosequence plots was applied to the species found around remnant and reference trees. The proportion of old growth specialists and generalists around remnant trees is significantly greater than around reference trees, and the proportion of second growth specialists is significantly greater around reference trees than occur around remnant trees. Although remnant trees may initially accelerate secondary forest growth, no evidence suggests that they locally affect stem density and basal area at later stages of regrowth. Remnant trees do, however, have a clear effect on the species composition of the surrounding forest, even after 20-30 years of forest growth.

Keywords: succession, biodiversity, functional diversity, reproductive trait, dispersal, pollination, seed size, remnant tree, isolated tree, relic tree, tropical forest, forest regeneration, conservation, assisted regeneration

CHAPTER 1:

Recovery of species diversity and reproductive trait diversity along a successional chronosequence

Introduction

Tropical forest continues to be converted to a variety of anthropogenic land use types, causing significant losses of local and regional biodiversity and ecosystem services. Recovery of some of these losses is possible through secondary forest regeneration following abandonment of agricultural land use (Guariguata and Ostertag 2001, Hassler *et al.* 2011), although the biodiversity value of regenerating forests remains a controversial issue (Gibson *et al.* 2011). Biodiversity encompasses taxonomic diversity, genetic diversity, phylogenetic diversity, and functional diversity. Reproductive traits are species-specific functional traits that are strongly linked to demography and life history. Because most reproductive traits are response traits – functional traits that influence responses to disturbance and changes in resource availability (Naeem and Wright 2003), they are likely to change in tree communities during succession. Niche-based theories of community assembly propose that functional traits of species underlie patterns of species composition (Mayfield *et al.* 2005, Mouchet *et al.* 2010). Examining changes in reproductive traits over succession permits inferences regarding the factors that influence community reassembly following disturbance; examining patterns of diversity over succession permits inferences about whether or not the community is on a path to converge with the levels of diversity observed in old growth forests.

Reproductive traits of woody and herbaceous species vary between human-disturbed and forested habitats (e.g. Mayfield *et al.* 2005, Girao *et al.* 2007, Santos *et al.* 2008, Lopes *et al.* 2009), but few studies have compared species richness or species diversity and reproductive trait diversity between secondary and old growth forest or during succession (e.g. Chazdon *et al.* 2003, Kimmel *et al.* 2010, Piotto *et al.* 2009, Lohbeck *et al*. 2012). Our study is the first to look at multiple aspects of species and reproductive trait diversity, and their relationship to each other,

across a successional chronosequence. We focused on pollination method, diaspore dispersal mechanism, fruit size, and diaspore size as key reproductive traits. These traits have obvious importance to successional processes. Succession is a landscape process on a timescale of decades to centuries, so pollination and dispersal are essential for colonization and recruitment over long time scales. Successful pollination is required for a species to be able to disperse, for persistence of a species in an area, and for maintenance of genetic diversity. Fruit size (particularly for fleshy fruits consumed by vertebrates) influences interactions with the disperser or dispersal mechanism – how far it can be carried or propelled and how long it spends in an animal's digestive tract (Fukui 2003). Most diaspores are dispersed near the parent plant, but if a parent plant cannot reproduce, the persistence of a species locally depends on the input of diaspores from further away. Diaspore dispersal often depends on other organisms or on wind and determines whether or not a species is dispersed into a successional area. Diaspore size determines how likely the diaspore is to survive once it arrives, but a trade-off exists with how many diaspores arrive in the area. Multiple, smaller diaspores with low rates of establishment may have similar rates of overall survival compared with fewer large diaspores with high rates of establishment (Schupp 1995, Moles and Westoby 2004). Diaspore dispersal and associated traits (like diaspore size) are widely recognized as major contributors to community assembly (e.g., Hubbell 2001, Pavoine *et al.* 2010).

Because succession is a lengthy process, our study used a place-for-time substitution. We relied on multiple measures of biodiversity, taxonomic and functional (reproductive traits), to compare tropical wet forest communities at different stages of succession. We asked a number of questions. How does functional diversity change with succession? What functional traits are associated with particular successional stages? What functional traits are associated with species

rarity and abundance? How does reproductive trait diversity vary across successional stages? What is the relationship between species richness and reproductive trait diversity along a successional chronosequence? As species richness increases along the chronosequence, which previous studies have shown is often the case (e.g., Halpern *et al.* 1995, Pena-Claros 2003, Capers *et al.* 2005, Tran *et al.* 2010), functional diversity may increase as well, but this relationship depends on processes of community assembly (Mayfield *et al.* 2005, Mouchet *et al.* 2010). If limiting similarity is driving community assembly, we expect increasing levels of functional diversity through succession. If niche filtering is more important, we expect high functional turnover but low levels of functional diversity throughout the chronosequence. Neutral processes yield intermediate levels of functional diversity that show no obvious trend through the chronosequence (Mouchet *et al.* 2010).

Methods

Site Description

We conducted our research on the Osa Peninsula, Costa Rica. The forests of the Osa Peninsula support the soaring canopies of tree species exceeding 60 m in height, with similar generic compositions to the Colombian Amazonian regions (unlike forests in the rest of Costa Rica), and high levels of diversity and endemism (Janzen 1983, Aguilar *et al.* 2008, Barrantes *et al.* 1999). Our study plots were located in the state of Puntarenas, at Río Piro, Matapalo, Los Mogos and Bahía Chal (Fig. 1). Río Piro is halfway between Puerto Jiménez and Carate, which is near the southern entrance to Corcovado National Park. Matapalo is on the southeastern most point of the Osa Peninsula, near where the Golfo Dulce meets the Pacific Ocean. Los Mogos and Bahía Chal are both near the northwestern shore of the Golfo Dulce. The study consisted of

nineteen 0.5 ha plots (50 m x 100 m) of different ages (5 plots of 5-14 years since pasture abandonment, 4 plots of 15-30 years, 5 plots of 31-50 years, and 5 plots of old growth forest) distributed among the four sites (Table 1). All secondary plots were former cattle pasture. Originally we established 20 chronosequence plots, but one plot was excluded due to the discovery of prior selective logging. Plots were assigned age classes based on examination of aerial photographs and interviews with local landholders.

Seventeen plots were located in lowland tropical wet forest, with plots 11 and 14 in a cloud forest transition zone. All plots were embedded in a predominantly forested matrix. Río Piro and Matapalo experience rainfall of 4500-5000 mm per year, with a three month dry season. Los Mogos and Bahía Chal receive 3500-4000 mm of rain per year, with a one month dry season. The average daily temperature for sites ranges from 23 to 27˚C (Morales *et al.* 2012).

Vegetation sampling

We collected data in the field from October 2010 to May 2011. In all plots, we identified to species, counted, and measured the diameter of each stem ≥ 5 cm diameter at breast height (dbh). We also noted the condition of the stem. Only 97 stems out of 9030 were unidentified to any taxonomic level beyond eudicot. Most unidentified stems were 5-8 cm dbh, with 6 larger (but none larger than 35 cm dbh). Fifty stems that were identified only to genus were excluded for the species-level analyses. Identifications to all taxonomic levels, including morphospecies, were performed by experienced regional botanists overseen Reinaldo Aguilar, an expert in the flora of the Osa Peninsula, who also collected voucher specimens.

Soil sampling

We took three 10 cm deep soil samples from points 10 m apart in the center of the plots between February and March of 2012. We homogenized the three samples, dried them at 50˚C for 48 hours, and sieved them (method as per Cory Cleveland; Rebecca J. Cole, pers. comm.) Brookside Laboratory analyzed all samples for total exchange capacity (ME/100g), soil pH, percent organic matter, estimated N release (lbs. N/acre), S (ppm), P (mg/kg), Ca (mg/kg), Mg (mg/kg), K (mg/kg), Na (mg/kg), percent H, B (mg/kg), Fe (mg/kg), Mn (mg/kg), Cu (mg/kg), Zn (mg/kg), and Al (mg/kg).

Trait data collection

We compiled the reproductive trait database using books, articles and herbarium specimens (National Biodiversity Institute [INBio], George Safford Torrey Herbarium [University of Connecticut], and Harvard University Herbaria). We also used information contained on the Tropicos website (www.tropicos.org, maintained by the Missouri Botanical Garden), the Smithsonian Tropical Research Institute (STRI) Herbarium website (http://biogeodb.stri.si.edu/herbarium/), and the Flickr page of Reinaldo Aguilar (http://www.flickr.com/photos/plantaspinunsulaosa/). If information to species could not be found for diaspore size, diaspore disperser, or pollinator, information from congeners was applied, as these traits are generally conserved within a genus (15.8% of species were scored in this way for diaspore length, 49.7% of species for dispersal method, and 48.8% of species for pollination mode). Information at the family level was occasionally used when there was evidence in the literature that pollination system was conserved within a given family (18.1% of species).

Forest structure analysis

We calculated average tree density and total basal area for each plot. Total basal area was calculated using the standard forestry formula ($\pi*(\frac{dbh}{2})^2$, summed for each plot). We ran two-way ANOVAs for average tree density and total basal area, grouping plots by age (5-14 yrs., 15-30 yrs., 31-50 yrs., old growth forest) and by site (Río Piro, Matapalo, Los Mogos and Bahía Chal). Because total basal area significantly increases across the chronosequence, we used it as a continuous variable proxy for age in most subsequent analyses of species richness, species diversity, and functional traits. Stand basal area has been shown to be a good replacement for age in other studies of tropical forest succession (Lohbeck *et al*. 2012), but to control for possible non-linearity in basal area between second-growth and old-growth forest plots, we only performed linear regressions with second-growth forest plots only.

Classification analysis

To classify the tree species in our plots into successional age specialist and generalist groups, we followed the procedure for classifying species as specialists or generalists in two habitat types developed by Chazdon *et al*. 2011. We conducted an analysis of old-growth (OG) versus second-growth (SG) specialists in CLAM (http://chao.stat.nthu.edu.tw/softwarece.html) with p = 0.01 and K = 0.667 (as per Anne Chao's recommendation; Anne Chao pers. comm.) for all data. This analysis classified species into four successional classification groups based on abundance: second growth specialist ("SG Specialist"), old growth specialist ("OG Specialist"), generalist ("Generalist"), and Rare to classify ("Rare"). The abundances of all species in all second growth plots (ages 5-14 yrs., 15-30 yrs., and 31-50 yrs.) were combined for second growth, and the abundances of all species in all old-growth plots were input as old growth.

Species abundance, species evenness, species richness, species diversity, and family richness analyses

We first compared the total relative abundances of species in each forest age class. Evenness was calculated using Hill evenness ($\frac{Shannon\ exponential\ diversity}{\ln(number\ of\ species)}$) (Jost *et al.* 2011). We used EstimateS Version 9 (http://viceroy.eeb.uconn.edu/estimates/) to estimate extrapolated species richness to a common target of 718 individuals, the greatest number of individuals in any single plot, and computed 95% confidence intervals for species richness for each plot. We also used EstimateS to calculate rarefied Shannon exponential diversity for each plot at 218 individuals, the greatest common number of individuals for all the plots. To calculate family richness, we counted the number of families found in a single plot. We ran linear regression analyses of species evenness, species richness, species diversity, and family richness versus basal area. We also created rank-abundance curves for each forest age class.

Diaspore size and fruit size

We used diaspore length or fruit length as proxies for diaspore size and fruit size, respectively. If diaspore or fruit length was listed as a range in the literature or was measured as a range of lengths at one of the herbaria (the most common case), we used the midpoint of that range ($\frac{min+max}{2}$) because we did not have enough information to construct a true intraspecific size range. We created a list of diaspore and fruit sizes for each plot, in which the number of entries for each species matched the abundance of that species found in that plot. We calculated the median and mode of these non-normal distributions for each plot, as well as 95% of the range (the 0.975 quantile minus the 0.025 quantile of these distributions). We performed a linear

regression of diaspore size or fruit size (as represented by median, mode, or 95% range) against total plot basal area (a proxy for total stand age). We also used the FD package in R (http://cran.r-project.org/web/packages/FD/) to calculate the community weighted mean (CWM) of diaspore size and fruit size. These CWMs were used in a linear regression analysis against total plot basal area, a proxy for successional age.

Diaspore dispersal method and pollination method analyses

Diaspore dispersal mode was binned into four categories: animal, explosive, wind, and gravity dispersal, following Chazdon *et al*. (2003). Pollination mode was binned into five categories: bat, bat/insect, bird, bird/insect, insect, wind, and multiple. Species pollinated by a specialized insect or multiple insects were binned into "insect". Species with three or more types of pollinators, such as moth, bat, and other mammal, were binned into "multiple". Our sources did not provide enough information to separate generalist and specialist pollinators effectively. We also recognize that because all visitors to flowers are not pollinators, and thorough studies for most species are lacking, some species classified as multiple might be misclassified due to scant information. This effect could positively bias the number of plant species in this pollination category. For the disperser or pollinator by age analysis, we performed the analysis at the level of individuals. We used an analysis of multinomial proportions to determine whether proportions of individuals in different dispersal and pollinator categories varied significantly across forest age classes.

Reproductive trait by classification analyses

We used ANOVAs to determine whether diaspore and fruit sizes differed across specialist and generalist categories (SG Specialist, Generalist, OG Specialist, and Rare). For the disperser or pollination mode by successional classification analysis, we used an analysis of multinomial proportions, similar to the one we used for proportions of dispersal and pollinator by age class. In this analysis, however, proportions did not incorporate individual abundance information, only number of species, as our question focused on what patterns we found for species within the classification types.

Functional diversity analyses

To calculate functional diversity of diaspore dispersal method or pollination for each plot, we treated each diaspore dispersal method or each pollinator as a taxon unit. We used these diaspore dispersal methods or pollinators and their associated abundances in each plot as input to EstimateS and calculated Shannon exponential diversity for diaspore dispersal and pollination in each plot. These diversities were used in a linear regression for each reproductive trait versus basal area. We computed diaspore size and fruit size diversity using the index FD_{var} (Smith and Wilson 1996), which is a single dimension functional diversity index that accounts for continuous trait diversity and abundance. We also used the multidimensional functional diversity indices F_{Ric} (functional richness), F_{Eve} (functional evenness), F_{Div} (functional divergence), and Rao's Q (functional diversity) found in the "FD" package for R (Mouchet *et al.* 2010), which combine diaspore and fruit size. We used the calculated diversities in a linear regression for each reproductive trait versus basal area. We then created Pearson correlation analyses for each reproductive trait diversity measure versus species richness across the 19 plots.

Soil and spatial autocorrelation analyses

To verify that the patterns due to successional changes were not a consequence of soil conditions or other conditions in the plots, we created a series of multiple linear regressions in R of soil elemental variables as a function of basal area, stem density, species diversity, and species richness, each with a random effect term for location. Soil elemental variables were chosen because of their impact on plant growth and reproduction: N (represented by estimated N release), K, Ca, Mg, P, Fe, B, and pH. To assess the degree to which our results were might be influenced by spatial autocorrelation, we created a variogram for every structure, richness, evenness, and diversity measure we used, including those for reproductive traits.

Results

Forest structure and soil

We measured a total of 9030 individuals over the 19 plots. Across the chronosequence, stem density showed no significant pattern ($p > 0.05$), whereas total basal area increased significantly ($p << 0.001$). We found no significant differences in any soil element over different age classes or between the four different study areas ($p > 0.05$). Species diversity, species richness, basal area, and stem density were not significantly related to N, K, Ca, Mg, P, Fe, B, or pH, nor were they significantly related to our random effect variables for location ($p > 0.05$ for all). We found no evidence of spatial structure in most of our forest structure and reproductive trait diversity measurements. We did find a suggestion of spatial autocorrelation in our species richness, species evenness, species diversity, and family richness, as well as in Rao's Q, F_{Dis}, F_{Ric}, and fruit size diversity. This possible spatial autocorrelation in species or family diversity measures was likely due to one outlier plot that was also separated geographically from the other

plots. Because it was an old-growth plot, it was not included in our linear regressions (no old growth plots were included) and therefore should not bias our results.

Classification

We found a total of 464 species or morphospecies in the 19 plots. Forty-six species were classified as "SG Specialists", 44 species were classified as "OG Specialists", 41 species were classified as "Generalists", and the rest of the 333 species were classified as "Rare" (Appendix 1). Any species classified in the Rare category had no more than 16 individuals in all 19 plots combined (average number of individuals was 3.7). As plots increased in age, the proportion of Rare individuals increased (9.25% in 5-14 yr. old forest, 10.5% in 15-30 yr. old forest, 14.0% in 31-50 yr. old forest, 18.9% in old growth forest, Fig. 2) because the proportion of Rare species increased.

Species abundance, species evenness, species richness, species diversity, and family richness

Of the 9030 individuals over all our plots, 8933 were identified to at least genus and 8883 were identified to species or morphospecies. The 5 most abundant species composed 43.4% of the total abundance in 15-30 year-old plots, 24.4% of the total abundance in 5-14 year-old plots, 23.0% of the total abundance in 31-50 year-old plots, and 22.8% of the total abundance in old-growth forest plots (Fig. 3). These abundance patterns reflect differential dominance in each of the age classes, which our analysis of Hill evenness confirmed. Species evenness (Hill evenness) increased as basal area, our proxy for plot age, increased ($R^2 = 0.313$, $p = 0.038$, Fig. 4a).

Extrapolated species richness and species diversity (Shannon exponential diversity) increased significantly with increasing plot basal area (richness: $R^2 = 0.632$, $p < 0.001$; diversity:

$R^2 = 0.368$, $p = 0.021$, Figs. 4b and 4c). Family richness (the number of families within a plot) also increased significantly with plot basal area ($R^2 = 0.598$, $p = 0.001$, Fig. 4d).

Diaspore size and fruit size

Median diaspore size and CWM of diaspore size both increased significantly with plot basal area (Table 2, Fig. 5a), but diaspore size mode and diaspore size 95% range did not. Diaspore size diversity (FD_{var}) showed a marginally significant increase with increasing basal areas (Table 2). Mean diaspore length was significantly smaller for SG specialists than any other successional classification type ($p << 0.001$, Fig. 5c). Generalist and Rare species had similar mean diaspore lengths with similar standard deviations.

In contrast with diaspore size, median fruit size and fruit size mode did not show a significant relationship with basal area (Table 2, Fig. 5b). Fruit size 95% range also had no significant relationship with basal area, nor did the CWM of fruit size (Table 2). Fruit size diversity (FD_{var}) significantly increased with increasing basal area (Table 2). Mean fruit length was significantly smaller in SG Specialist species than in any other successional classification type ($p << 0.001$, Fig. 5d). As with diaspore size, mean and standard deviations of fruit size were similar for Generalist and Rare species.

Diaspore dispersal method and pollination method analyses

Animal dispersal was by far the most abundant type of dispersal. Animal dispersal increased significantly with increasing age class, from 64% in 5-14 year-old plots to 93% in old-growth forest (Fig. 6a). Wind dispersal was the second most abundant dispersal mode. Wind dispersal had significantly greater abundance in 5-14 year-old and 15-30 year-old plots than 31-50 year-old plots, which had significantly more wind dispersal than old-growth plots. Explosive

dispersal was significantly greater in 5-14 year-old plots than in any other age class. Gravity accounted for a very small frequency of dispersal methods in all plots (Fig. 6a). Diversity of dispersal modes was not significantly related to basal area ($R^2 = 0.002$, $p = 0.882$).

Species with animal dispersal were significantly more abundant in Rare species than in SG Specialist species and OG Specialist species. Species with wind dispersal were significantly more abundant among SG Specialists than among Rare species. Species with explosive dispersal and gravity dispersal did not vary significantly across classification types (Fig. 6b).

Insect pollination was by far the most abundant pollination method (Fig. 7a); it was significantly greater in 5-14 year-old and 15-30 year-old plots than in 31-50 year-old and old-growth plots. Depending on age class, the next most abundant pollination method was bird/insect, multiple, or wind, with each of these accounting for 5-15% of abundance. Bird/insect pollination generally decreased through the chronosequence, with no significant difference in relative abundance between 5-14 year-old and 15-30 year-old plots. The abundance of individuals with multiple pollinators in 31-50 year-old plots was significantly greater than in any other age class. Wind pollination was significantly greater in old-growth plots than 31-50 year-old plots and significantly greater in 31-50 year-old plots than in 5-14 year-old and 15-30 year-old plots. Bird pollination generally increased through the chronosequence, with no significant difference in relative abundance between 5-14 year-old and 15-30 year-old plots. Bat/insect and bat pollination were generally the least abundant pollination methods. Bat/insect pollination was significantly greater in 31-50 year-old plots than in old-growth plots. No significant differences between age classes were found for bat pollination, although very small abundances of bat-pollinated species overall make any conclusions difficult (Fig. 7a).

The relative abundance of Generalist species with wind pollination was significantly greater than any other classification type. Bird/insect pollination had a significantly greater relative abundance for SG Specialist individuals than for any other classification type. The opposite was true for bird pollination; it had a significantly greater abundance for OG Specialist individuals than for any other classification type. Bat-pollinated individuals were significantly more abundant for OG Specialist and Rare species. Wind pollination was significantly more abundant for Generalist species than any other classification type (Fig. 7b). Pollination diversity was not significantly related to total basal area ($R^2 = 0.081$, $p = 0.325$).

Functional diversity and species diversity

Functional richness, diversity, and evenness were not significantly related to basal area. Species richness was significantly correlated with dispersal diversity, with dispersal diversity decreasing with increasing species richness (cor = -0.47, $p = 0.040$, Fig. 8a). Species richness was marginally correlated with pollination diversity, with pollination diversity increasing with increasing species richness (cor = 0.404, $p = 0.086$, Fig. 8b). Diversity of diaspore size and fruit size did not show a significant correlation with species richness (diaspore size diversity: $p > 0.5$, fruit size diversity: $p > 0.1$). Functional richness (F_{Ric}) was significantly positively correlated with species richness (cor = 0.488, $p = 0.034$). No other measures of functional diversity were significantly correlated with species richness (all $p > 0.05$).

Discussion

Biotic interactions are an essential part of rain forest tree reproduction. In all forest types we surveyed, over 60% of individuals were dispersed or pollinated by animals (Fig. 6). We

found a large increase in the overall percent of animal diaspore dispersal as successional age increased (Fig. 6a). Dispersal diversity also decreases with increasing species richness. This indicates that strong niche filtering acts on species with animal dispersal as succession progresses. Animals play a much greater role in later successional stages than in early secondary forest in determining where species are locally distributed. Interestingly, our results do not show a corresponding pattern in pollination. The percent of individuals with wind pollination increases with successional age, although it makes up only a small percentage of all pollination in old growth forest (< 10%, Fig. 7a). The diversity of pollinators marginally increases with increasing species richness, but not with basal area. These results show that as succession progresses, and as a greater diversity of trees grows in successional areas, more kinds of animals are involved in the pollination processes. Our results indicates that limiting similarity or neutral assembly processes are important in pollination mechanisms instead of the niche filtering processes that appear to be more important for dispersal mechanisms.

Our results are similar to those of Chazdon *et al.* (2003) and Piotto *et al.* (2009) in patterns of animal dispersal and pollination method between secondary and old growth forest, or across the chronosequence. Both studies found that animal dispersal is more common in old-growth forests than in secondary forests, with Piotto *et al.* finding that the frequency of animal dispersal increases with increasing age along the chronosequence. As animal dispersal frequency increases, wind dispersal (or "other" dispersal, as categorized by Piotto *et al.*, who pooled wind and explosive dispersal) decreases in frequency. Angel Muñiz-Castro *et al.* (2012) also found a decrease in wind-dispersed species across an 80-year chronosequence of tropical forest in Mexico. Chazdon *et al.* (2003) found that insect pollination was more frequent in secondary forest than old growth forest, which we found as well, with the exception of the oldest second

growth forest sites (31-50 years old). Chazdon *et al.* (2003) also found that wind pollination was more frequent in old-growth forest sites than in second growth forest sites.

Pollination diversity was marginally correlated with species richness in a positive direction, and seed dispersal diversity was significantly correlated with species richness in a negative direction. The only other measure of functional diversity that was significantly correlated with species richness was functional richness (F_{Ric}), using a combined measure of diaspore size and fruit size. Increasing species richness does not necessarily correspond with an increase in functional diversity, and depending on the functional trait, increasing species richness could actually correspond with a reduction in functional diversity. This complicated relationship indicates that different community assembly processes act on different aspects of plant reproductive traits as succession progresses, even when those reproductive traits are linked.

Our approach had several limitations for determining community assembly processes. First, we did not have enough information to divide animal dispersal into finer categories such as bird, bat, or monkey. Because both pollination and seed dispersal are overwhelmingly animal-mediated processes, finer categories of animal dispersal may have revealed a relationship between dispersal diversity and species richness. Second, our method for distinguishing niche filtering and limiting similarity from neutral processes, where neutral processes result in an intermediate relationship or no relationship between species richness and reproductive trait diversity, makes it impossible to distinguish a lack of pattern from the results of neutral processes. Null models and randomization have been used to separate neutral processes from niche process in the relationship between species richness or species diversity and functional trait diversity (Mayfield *et al.* 2005, Mouchet *et al.* 2010, Lohbeck *et al.* 2012, Raevel *et al.* 2012). Future analysis where we combine null models and randomization of the data would lead to

stronger conclusions about community assembly processes and how they affect reproductive traits.

Phylogenetic analyses of a community can illuminate community assembly processes (Kraft et al 2007, Cavender-Bares et al 2009). Phylogenetic analyses of successional communities suggested that habitat filtering (niche filtering) may be more important early in succession whereas biotic interactions may be more important later in succession (Letcher *et al.* 2012). Phylogenetic analyses of our chronosequence plots paired with our reproductive trait analyses could help determine which community assembly processes are acting over the course of succession on which reproductive traits (Letcher *et al.* 2012).

In our current understanding of succession, early successional species have small seeds and are distributed by wind or flying vertebrates (i.e. Foster and Janson 1985, Ibarra-Manriquez and Oyama 1992, Clark and Clark 1992, Dalling *et al.* 1998). Few studies have looked at how these attributes change during succession. Individuals found in early second growth forests do have smaller seeds and smaller fruits, and a higher proportion are dispersed by wind than at any other stage (Fig. 5 and 6). As age of succession increases, seeds become larger (Fig. 5), with an increasing percentage of animal dispersal and a corresponding decreasing percentage of wind dispersal (Fig. 6). Interestingly, seed size and fruit size differentiation exists only between SG Specialist species and all other species. Generalists, OG Specialists, and Rare species do not differ significantly from each other in either seed size or fruit size. The lack of difference between Generalists and Rare species for seed or fruit size or dispersal mode suggests that these traits are not driving differences in the relative abundances of these two successional classification types. The only significant difference we found in reproductive traits between the two successional classification types was in pollination mechanism, but as the difference was

wind pollination, which would not be assumed to be a limiting factor, we conclude that other factors beyond the scope of our study explain the differences in abundance between these two classification groups.

The successional pattern for fruit size appears to be more complicated than for diaspore size (Fig. 5). While the mean fruit size of SG Specialist individuals is significantly smaller than the mean fruit size of OG Specialist individuals, no significant relationship exists for fruit size with successional age. Some of the wind-dispersed species have large wings that enhance the size of the fruit or the capsule in which the diaspores with wings are initially contained. *Inga* species, with their long, bean-like fruits, are more prevalent in secondary forests than they are in old growth forests (R. Aguilar, pers. comm.), and the size of their fruits contributes to the overall lack of trend.

In contrast to the findings of Lopes *et al.* (2009) and Santos *et al.* (2008) in the Atlantic forest region of Brazil, where secondary forests were relatively poor in species and reproductive traits, species and reproductive traits are recovering rapidly across the chronosequence in the Osa Peninsula. The 31-50 year-old plots are similar to or indistinguishable from old-growth plots in terms of species richness, species diversity, and reproductive traits. Old-growth plots are higher in species richness, species diversity, and species evenness than the linear trend of the second growth plots, although the appearance of a much higher mean is due to a singular, possible outlier plot. Other measures of diversity, such as family richness and median diaspore size, were similar between second-growth and old-growth plots. Not only are the secondary forests in our region recovering to nearly old growth forest levels of diversity, they are doing so in a relatively short period of time.

One major difference between the Osa study and Atlantic forest studies could be the effect of landscape. Lopes *et al.* (2009) and Santos *et al.* (2008) conducted their study in an area where nearly all of the forest in the landscape had been converted to other land use types, which could slow forest recovery. In our study region, a large part of the forested landscape is still intact. We did not have enough plots to determine whether or not surrounding landscape matrix influenced the species richness, diversity, and reproductive traits of our plots, but future studies of species and reproductive trait diversity over succession should incorporate the amount of intact forest in the landscape as a variable.

Gibson *et al.* (2011) recently claimed that conservation priority in tropical forest regions should be placed primarily on old-growth forest, based on their meta-analysis of pairwise comparisons between the biodiversity of old-growth and disturbed forests. Although our analyses support the view that secondary forests are less diverse in terms of both taxonomic diversity and reproductive trait diversity than old-growth forests, our results also show that secondary forests are on a trajectory towards convergence with the nearby old-growth forests. While old-growth forests are certainly important for species conservation, second-growth forests have a high conservation value as well for both their unique suite of species (SG Specialists) and their potential to recover the species and trait diversity found in old-growth forests. If there are areas of old-growth forest nearby, second growth forest recovers rapidly its similarity of species composition to old growth forest (Chazdon et al. 2009, Dent and Wright 2009). Second-growth forest or recently abandoned pasture may be more extensive and less expensive land for conservation organizations to purchase than old-growth forest, allowing those organizations to purchase a mixture of old growth and current secondary forest which could ultimately yield a net increase in protected forested or future forested land. Loss of tropical forest continues at an

alarming rate, despite current conservation attempts, but hope remains in the form of secondary forests.

Tables

Table 1. Plot age and location information.

Plot No.	Age	Location		Plot No.	Age	Location
1	15-30	Piro		11	31-50	Mogos
2	Old Growth	Piro		12	5-14	Mogos
3	Old Growth	Piro		13	Old Growth	Mogos
4	31-50	Piro		14	5-14	Mogos
5	15-30	Piro		15	31-50	Piro
6	31-50	Piro		16	31-50	Piro
7	5-14	Matapalo		17	5-14	Bahia Chal
8	Old Growth	Matapalo		18	15-30	Bahia Chal
9	15-30	Matapalo		20	5-14	Bahia Chal
10	Old Growth	Bahia Chal				

Table 2. Results for linear regressions of various measures of diaspore or fruit size and diversity against basal area. Significant p-values are in bold.

Measure vs. Basal Area	**R^2**	**p**	**range (cm)**
Diaspore size median	0.393	**0.016**	~ 0.3-1.8
Diaspore size mode	0.168	0.146	~ 0.1-2.3
Diaspore size 95% range	0.162	0.154	~ 1.9-4.6
Diaspore size CWM	0.393	**0.016**	~ 0.4-1.9
Diaspore size diversity (FD_{var})	0.246	0.072	NA
Fruit size median	0.139	0.19	~ 0.8-4.0
Fruit size mode	0.195	0.114	~ 0.4-6.0
Fruit size 95% range	0.079	0.332	~ 7.9-24.7
Fruit size CWM	0.006	0.791	~ 1.5-6.7
Fruit size diversity (FD_{var})	0.356	**0.024**	NA

Figures

Figure 1. Locations of sampling plots on the Osa Peninsula. Red dots are 5-14 year-old plots, orange dots are 15-30 year-old plots, blue dots are 31-50 year-old plots, and purple dots are old-growth forest plots. The inset is a map of Costa Rica with the area of the larger map of the Osa Peninsula outlined in black.

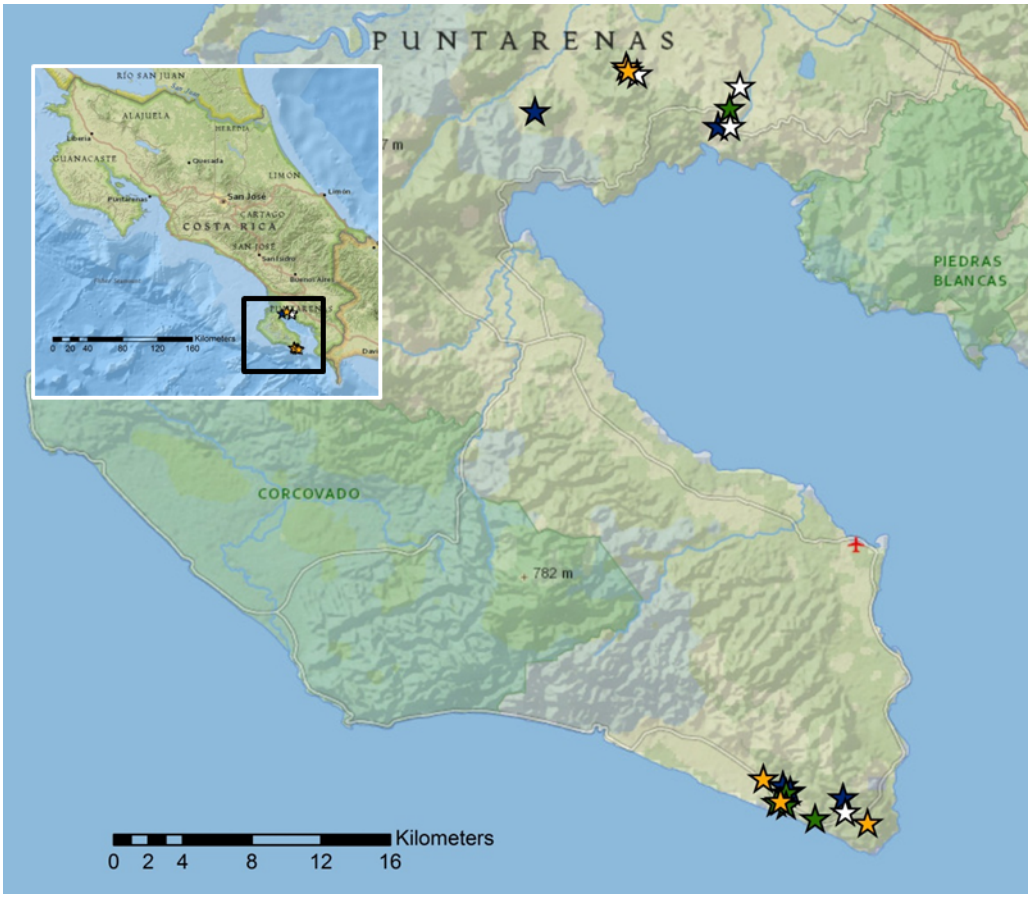


Figure 2. Total relative abundance of each classification type in each forest age class (summed per plot). “OG” stands for old growth forest. The proportions of each classification type for each age class sum to one.

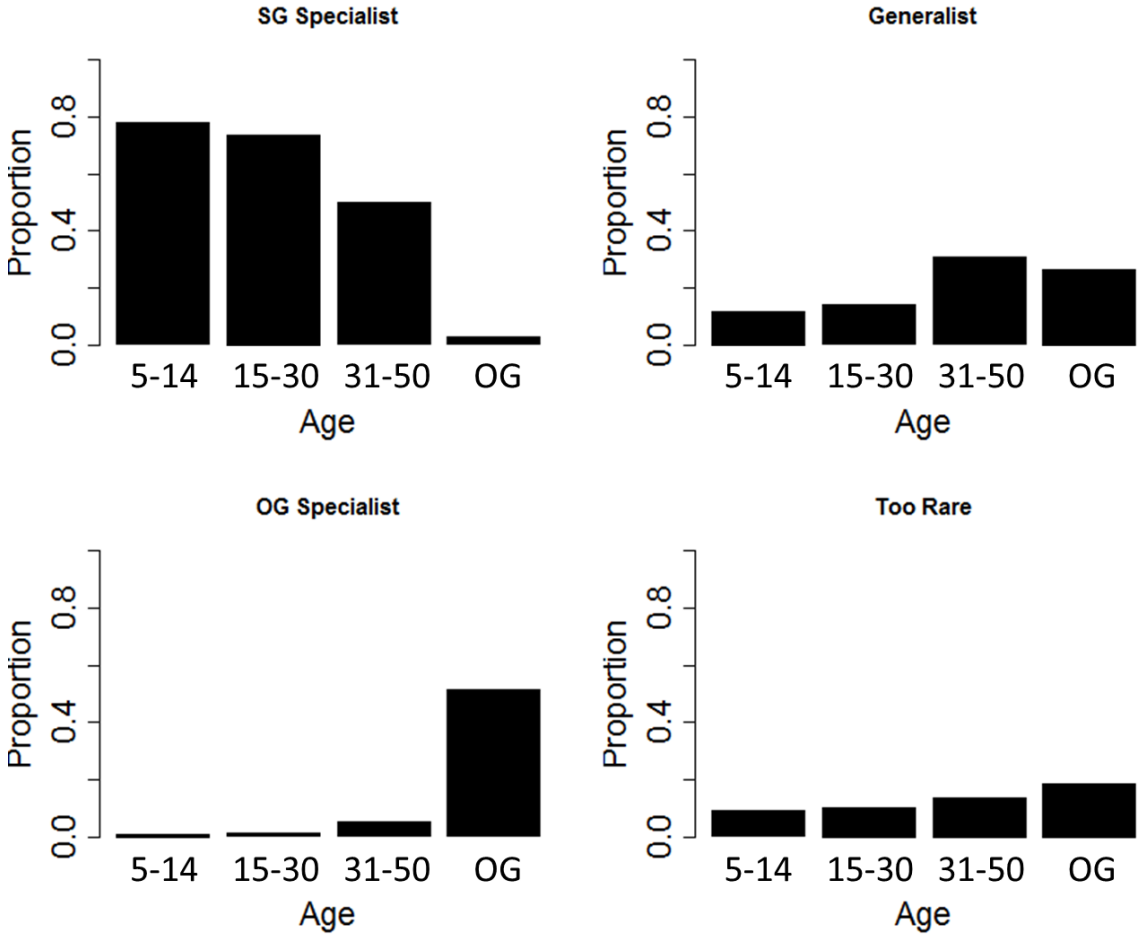


Figure 3. Rank-abundance curves for each age class. Red is 5-14 yrs., orange is 15-30 yrs., blue is 31-50 yrs., and purple is old growth forest. Both the y- and the x-axes are on a log scale.

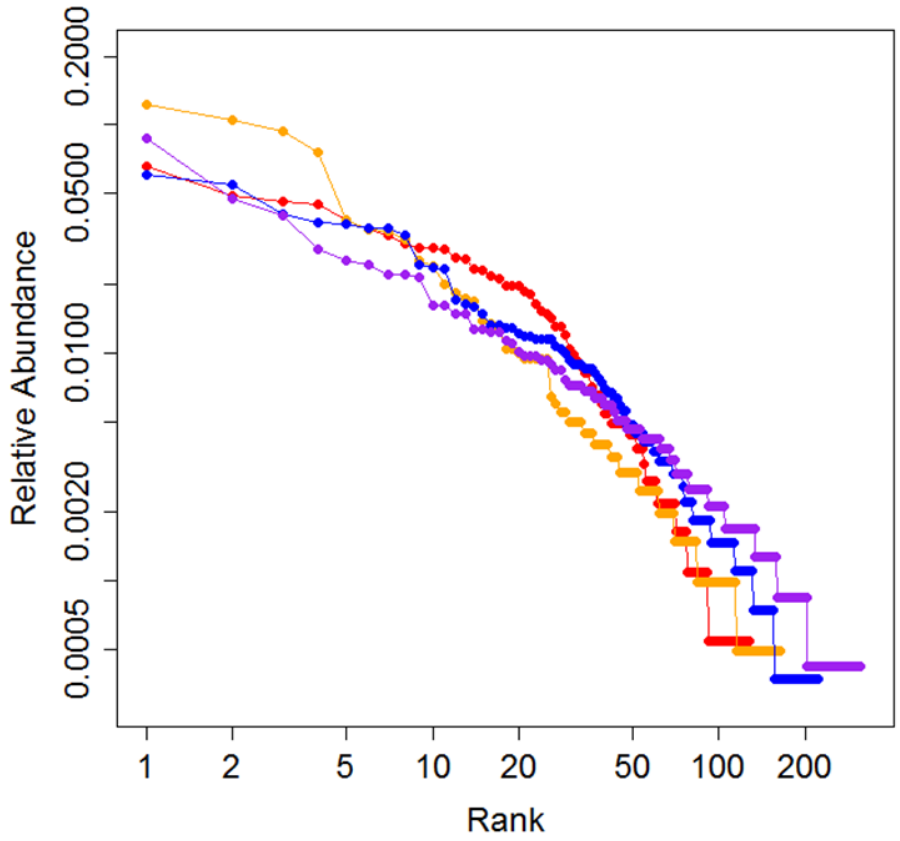


Figure 4. a.) Species evenness (Hill evenness) versus plot total basal area (m^2/ha). Linear regression is on second growth plots only; old growth points are shown for comparison. b.) Extrapolated species richness versus plot total basal area (m^2/ha). Linear regression is on second growth plots only; old growth points are shown for comparison. c.) Species diversity (Shannon exponential diversity) versus plot total basal area (m^2/ha). Linear regression is on second growth plots only; old growth points are shown for comparison. d.) Family richness versus plot total basal area (m^2/ha). In all plots, color of dot corresponds to age of forest plot. Linear regression is on second growth plots only; old growth points are shown for comparison.

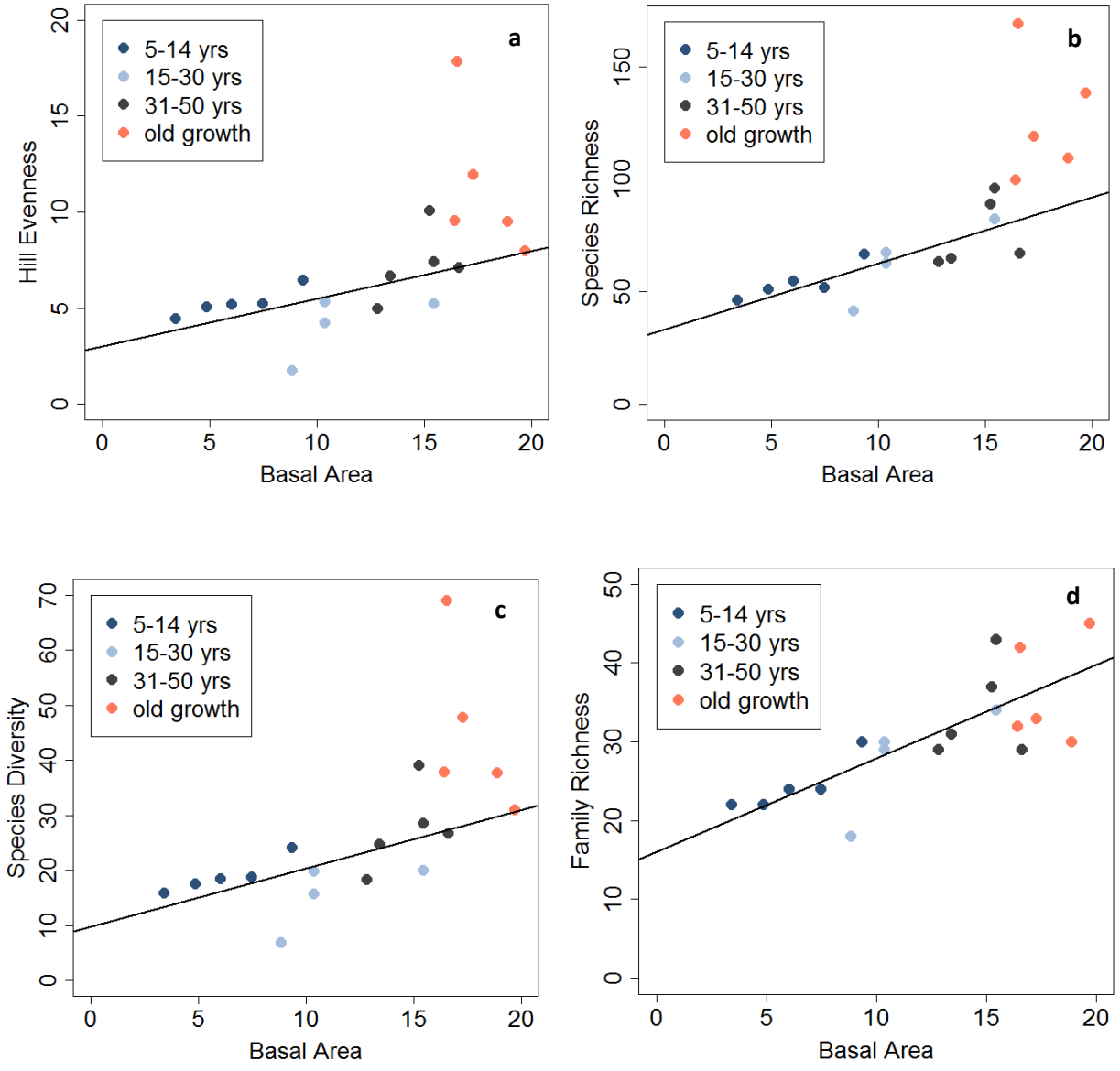


Figure 5. a.) Diaspore length median versus basal area. Linear regression is on second growth plots only; old growth points are shown for comparison. b.) Fruit length median versus basal area. Linear regression is on second growth plots only; old growth points are shown for comparison. c.) Mean diaspore length versus classification type. Error bars are ±1 standard deviation. The star indicates a significant difference between the mean of SG Specialists and all other successional classification types. d.) Fruit length versus classification type. Error bars are ±1 standard deviation. The star indicates a significant difference between the mean of SG Specialists and all other successional classification types.

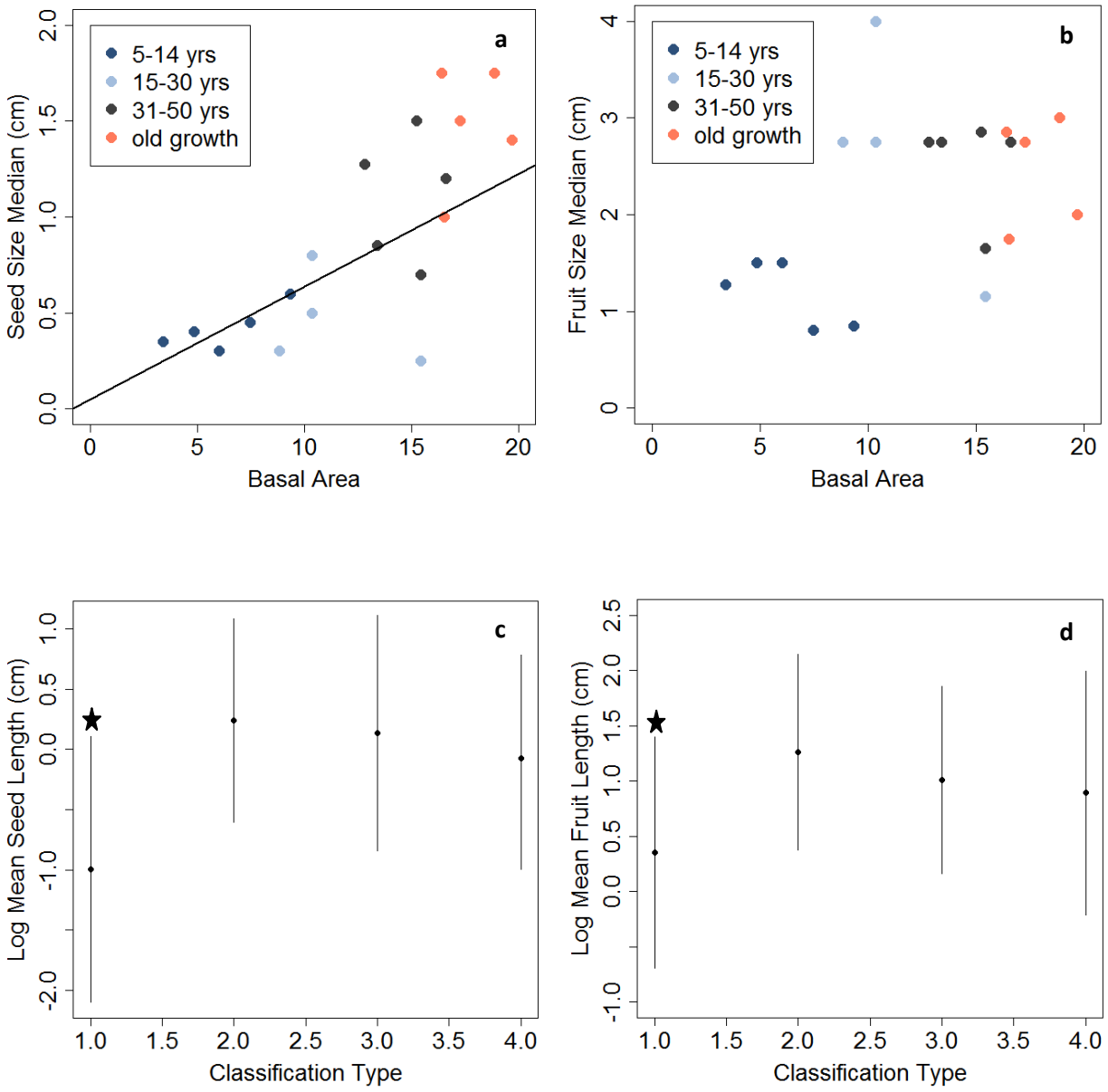


Figure 6. a.) Relative abundance of individuals with animal, explosive, gravity, and wind dispersal in each age class. All proportions of dispersal type for one age class sum to one. b.) Relative abundance of species with animal, explosive, gravity, and wind dispersal in SG Specialist, Generalist, OG Specialist, and Rare species. All proportions of dispersal type for one classification type sum to one.

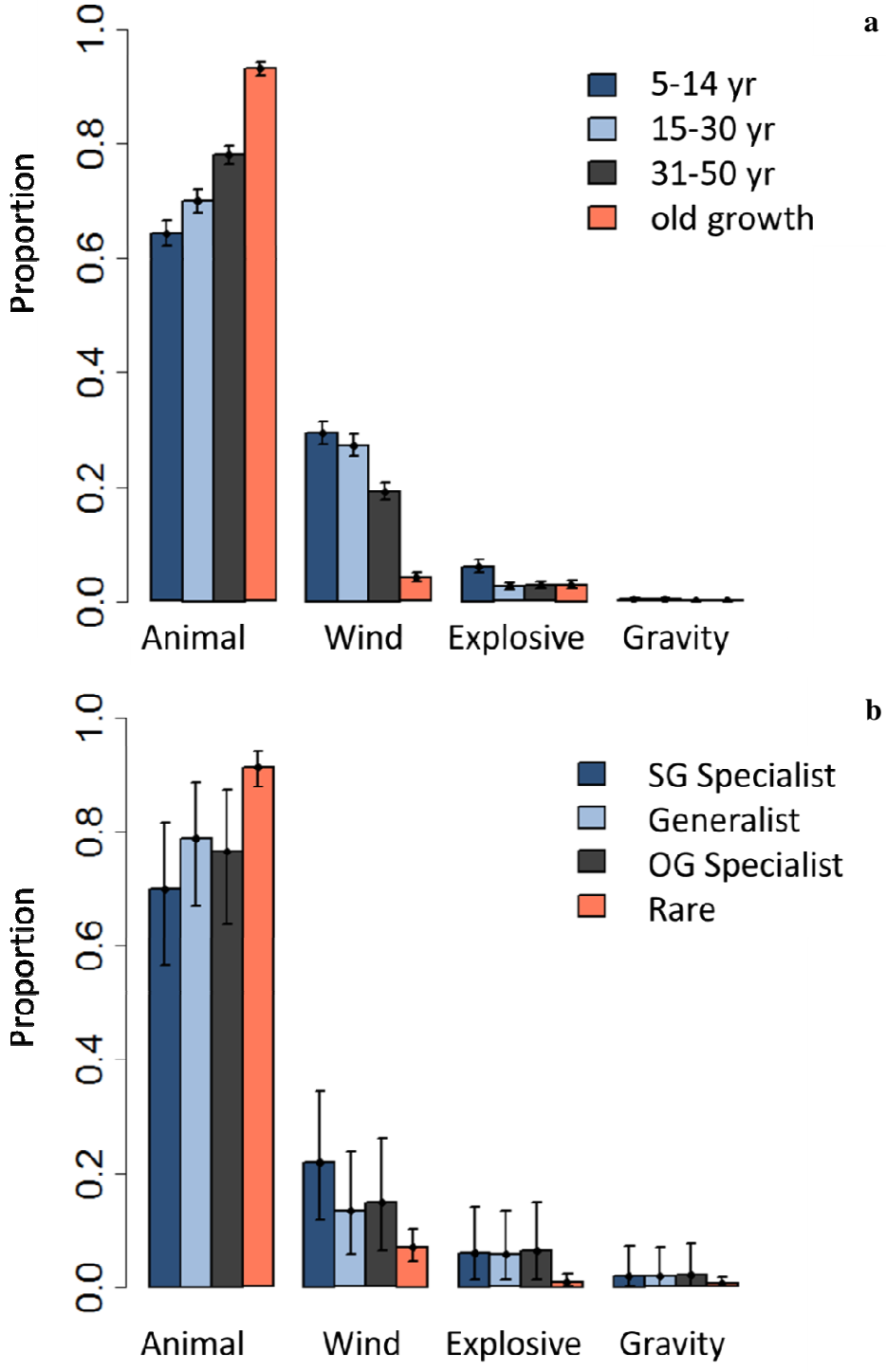


Figure 7. a.) Relative abundance of individuals with insect, bat/insect (Ba/In), multiple (Mult), wind, bird, bird/insect (Bi/In), and bat pollination in each age class. All proportions of pollination type for one age class sum to one. b.) Relative abundance of species with insect, bird/insect (Bi/In), wind, multiple (Mult), bird, bat/insect (Ba/In), and bat pollination in SG Specialist, Generalist, OG Specialist, and Rare species. All proportions of pollination type for one classification type sum to one.

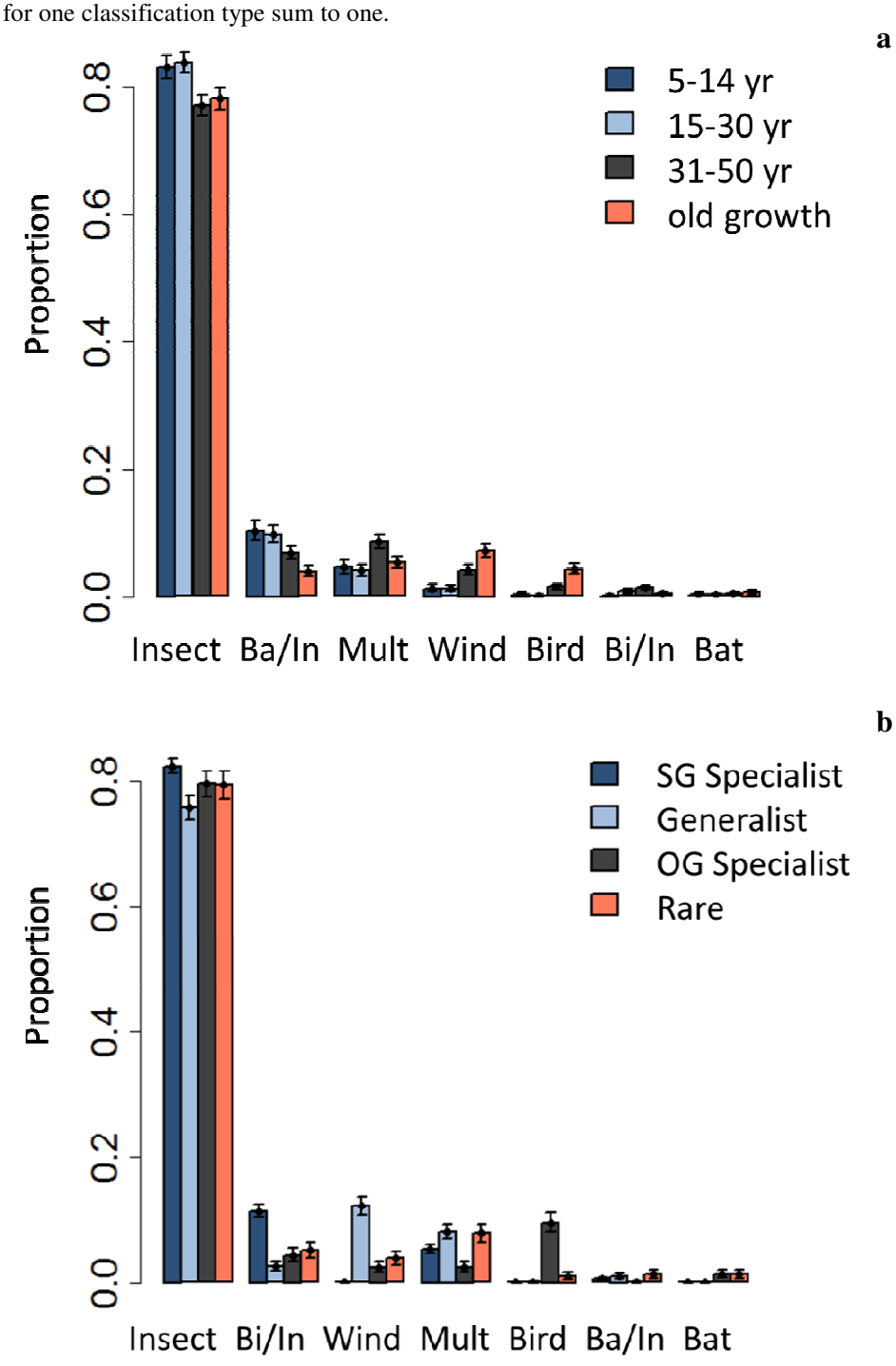
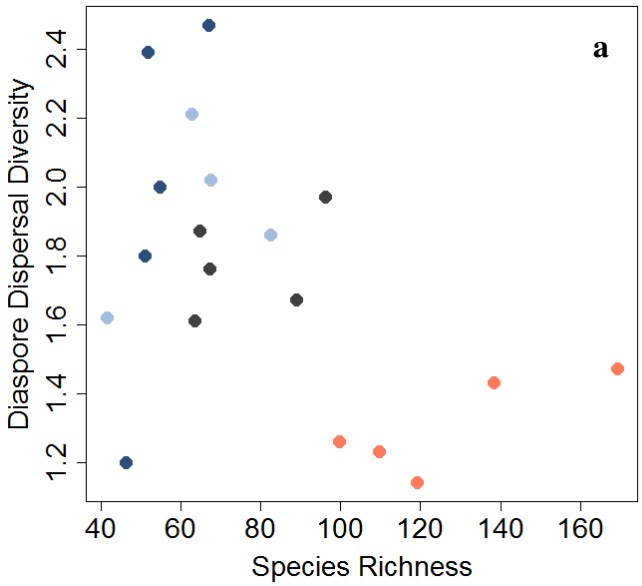
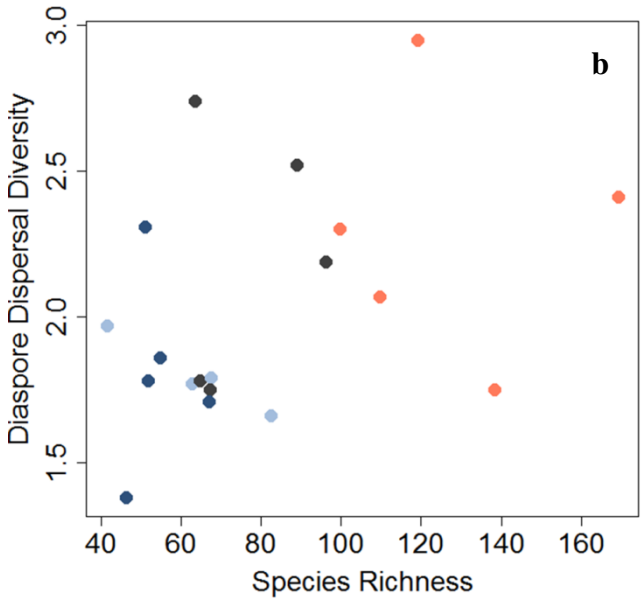


Figure 8. a.) Diaspore dispersal diversity versus species richness. The correlation between diaspore dispersal diversity and species richness is statistically significant and negative (cor = -0.468, p = 0.043) b.) Pollination diversity versus species richness. The correlation between pollination dispersal diversity and species richness is marginally significant (cor = 0.404, p = 0.086).





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Appendix

Appendix 1. List of species classified as SG Specialist, OG Specialist, and Generalist.

SG Specialist		Generalist		OG Specialist	
Species	**Family**	**Species**	**Family**	**Species**	**Family**
Alchornea costaricensis	Euphorbiaceae	*Anaxagorea crassipetala*	Annonaceae	*Amphirrhox longifolia*	Violaceae
Apeiba tibourbou	Malvaceae	*Aspidosperma spruceanum*	Apocynaceae	*Ampelocera macrocarpa*	Ulmaceae
Callicarpa acuminata	Lamiaceae	*Astrocaryum standleyanum*	Arecaceae	*Ardisia dunlapiana*	Primulaceae
Casearia arborea	Salicaceae	*Bombacopsis sessilis*	Malvaceae	*Batocarpus costaricensis*	Moraceae
Casearia sylvestris	Salicaceae	*Brosimum guianense*	Moraceae	*Caryocar costaricense*	Caryocaraceae
Chimarrhis latifolia	Rubiaceae	*Brosimum lactescens*	Moraceae	*Cheiloclinium cognatum*	Celastraceae
Chimarrhis parviflora	Rubiaceae	*Brosimum utile*	Moraceae	*Compsoneura excelsa*	Myristicaceae
Cordia bicolor	Boraginaceae	*Carapa nicaraguensis*	Meliaceae	*Dialium guianense*	Fabaceae
Croton smithianus	Euphorbiaceae	*Castilla tunu*	Moraceae	*Drypetes brownii*	Putranjivaceae
Cupania rufescens	Sapindaceae	*Cecropia insignis*	Urticaceae	*Duguetia confusa*	Annonaceae
Eschweilera biflava	Lecythidaceae	*Croton schiedeanus*	Euphorbiaceae	*Guarea bullata*	Meliaceae
Ficus insipida	Moraceae	*Dendropanax arboreus*	Araliaceae	*Guarea grandifolia*	Meliaceae
Goethalsia meiantha	Malvaceae	*Ficus maxima*	Moraceae	*Guarea tonduzii*	Meliaceae
Guazuma ulmifolia	Malvaceae	*Garcinia madruno*	Clusiaceae	*Guarea williamsii*	Meliaceae
Henriettea succosa	Melastomataceae	*Guatteria amplifolia*	Annonaceae	*Gustavia brachycarpa*	Lecythidaceae
Hieronyma alchorneoides	Phyllanthaceae	*Guarea pterorhachis*	Meliaceae	*Henriettea tuberculosa*	Melastomataceae
Inga multijuga	Fabaceae	*Heisteria acuminata*	Olacaceae	*Inga acrocephala*	Fabaceae
Inga thibaudiana	Fabaceae	*Heisteria concinna*	Olacaceae	*Iriartea deltoidea*	Arecaceae
Isertia laevis	Rubiaceae	*Inga alba*	Fabaceae	*Licaria misantlae*	Lauraceae
Lacistema aggregatum	Lacistemataceae	*Inga litoralis*	Fabaceae	*Mabea occidentalis*	Euphorbiaceae
Laetia procera	Salicaceae	*Jacaranda copaia*	Bignoniaceae	*Marila laxiflora*	Calophyllaceae
Laetia spA	Salicaceae	*Lacmellea panamensis*	Apocynaceae	*Miconia multispicata*	Melastomataceae
Lonchocarpus macrophyllus	Fabaceae	*Otoba novogranatensis*	Myristicaceae	*Naucleopsis ulei*	Moraceae
Luehea seemannii	Malvaceae	*Peltogyne purpurea*	Fabaceae	*Neea elegans*	Nyctaginaceae
Margaritaria nobilis	Phyllanthaceae	*Perebea hispidula*	Moraceae	*Ocotea pullifolia*	Lauraceae
Miconia affinis	Melastomataceae	*Protium panamense*	Burseraceae	*Pausandra trianae*	Euphorbiaceae
Miconia argentea	Melastomataceae	*Protium pecuniosum*	Burseraceae	*Pourouma bicolor*	Urticaceae
Miconia schlimii	Melastomataceae	*Pterocarpus violaceus*	Fabaceae	*Pouteria juruana*	Sapotaceae
Miconia trinervia	Melastomataceae	*Simarouba amara*	Simaroubaceae	*Pouteria laevigata*	Sapotaceae
Myriocarpa longipes	Urticaceae	*Simaba cedron*	Simaroubaceae	*Pouteria torta*	Sapotaceae
Nectandra umbrosa	Lauraceae	*Siparuna guianensis*	Siparunaceae	*Protium glabrum*	Burseraceae
Palicourea guianensis	Rubiaceae	*Tachigali versicolor*	Fabaceae	*Protium ravenii*	Burseraceae
Piper aduncum	Piperaceae	*Talisia nervosa*	Sapindaceae	*Protium schippii*	Burseraceae
Piper aequale	Piperaceae	*Tapirira myriantha*	Anacardiaceae	*Pseudolmedia spuria*	Moraceae
Psidium guajava	Myrtaceae	*Vantanea barbourii*	Humiriaceae	*Quadrella isthmensis*	Capparaceae
Psychotria grandis	Rubiaceae	*Virola koschnyi*	Myristicaceae	*Qualea polychroma*	Vochysiaceae
Siparuna gesnerioides	Siparunaceae	*Virola macrocarpa*	Myristicaceae	*Socratea exorrhiza*	Arecaceae
Siparuna sp1	Siparunaceae	*Virola sebifera*	Myristicaceae	*Sorocea pubivena*	Moraceae
Spondias mombin	Anacardiaceae	*Vochysia allenii*	Vochysiaceae	*Symphonia globulifera*	Clusiaceae
Terminalia amazonia	Combretaceae	*Xylopia macrantha*	Annonaceae	*Tabernaemontana longipes*	Apocynaceae
Tetrathylacium macrophyllum	Salicaceae	*Xylopia sericophylla*	Annonaceae	*Tetragastris panamensis*	Burseraceae
Trichospermum galeotii	Malvaceae			*Tovomita longifolia*	Clusiaceae
Trichospermum grewifolium	Malvaceae			*Unonopsis theobromifolia*	Annonaceae
Vismia baccifera	Hypericaceae			*Virola surinamensis*	Myristicaceae
Vochysia ferruginea	Vochysiaceae				
Warszewiczia coccinea	Rubiaceae				

Appendix 2. Reproductive traits by species. Additional references are as follows:
72. La Selva Digital Flora (http://sura.ots.ac.cr/local/florula3/index.htm)
73. Fruit and/or seed measured at The George Safford Torrey Herbarium (CONN)
74. Fruit and/or seed measured at Harvard University Herbaria
75. Fruit and/or seed measured at Instituto Nacional de Biodiversidad (INBio)
76. Fruit and/or seed measured in the field at La Selva Biological Station
77. Reinaldo Aguilar's Flickr photostream (http://www.flickr.com/photos/plantaspinunsulaosa/)
78. Southwest Environmental Information Network (SEINet) (http://swbiodiversity.org/seinet/)
79. Smithsonian Tropical Research Institute (STRI) Herbarium website (http://biogeodb.stri.si.edu/herbarium/)
80. Tropicos.org Missouri Botanical Garden (http://tropicos.org/)

Family	Genus species	Seed Length	Fruit Length	Disperser	Pollinator	Successional Classification	References
Actinidiaceae	*Saurauia yasicae*	0.1	0.65	Animal	insect	Too Rare	79; 72; 68; 74; 27
Anacardiaceae	*Anacardium excelsum*	2.8	3.05	Animal	Insect	Too Rare	79; 35; 79; 14; 13; 74; 60; 4
Anacardiaceae	*Spondias mombin*	2.5	2.75	Animal	Insect	SG Specialist	35; 71; 60; 4; 5
Anacardiaceae	*Spondias radlkoferi*	2	2.5	Animal	Insect	Too Rare	79; 14; 60; 14; 74; 4; 5
Anacardiaceae	*Tapirira myriantha*	1.75	1.5	Animal	multiple	Generalist	79; 10; 68; 19; 60; 4; 43
Annonaceae	*Anaxagorea crassipetala*	1.2	12	explosive	Insect	Generalist	10; 68; 27
Annonaceae	*Annona amazonica*	1.2	5.65	Animal	Insect	Too Rare	79; 10; 68; 76; 27; 43
Annonaceae	*Annona mucosa*	1	8	Animal	Insect	Too Rare	14; 68; 27; 43
Annonaceae	*Cymbopetalum costaricense*	1.25	7.75	Animal	Insect	Too Rare	10; 68; 14; 27
Annonaceae	*Desmopsis heteropetala*	1.15	3.5	Animal	Insect	Too Rare	77; 68; 79; 27; 32
Annonaceae	*Desmopsis verrucipes*	0.1	1.3	Animal	Insect	Too Rare	68; 79; 27; 32
Annonaceae	*Duguetia confuse*	1.5	4.5	Animal	Insect	OG Specialist	79; 19; 77; 27; 4
Annonaceae	*Guatteria amplifolia*	0.8	1.15	Animal	Insect	Generalist	79, 68; 72; 19; 79; 60; 27; 32
Annonaceae	*Guatteria chiriquensis*	1.15	0.95	Animal	Insect	Too Rare	14; 68; 19; 27; 32
Annonaceae	*Guatteria lucens*	0.8	NA	Animal	Insect	Too Rare	79; 19; 27; 32
Annonaceae	*Guatteria pudica*	1.15	0.95	Animal	Insect	Too Rare	14; 19; 27; 32
Annonaceae	*Guatteria rostrata*	1.15	NA	Animal	Insect	Too Rare	14; 19; 27; 32
Annonaceae	*Mosannona costaricensis*	1.25	1.75	Animal	Insect	Too Rare	77; 27
Annonaceae	*Oxandra venezuelana*	1.55	2.2	Animal	Insect	Too Rare	68; 60; 14; 79; 27
Annonaceae	*Unonopsis osae*	1.3	NA	Animal	Insect	Too Rare	77; 14; 27
Annonaceae	*Unonopsis theobromifolia*	0.12	1.85	Animal	Insect	OG Specialist	77; 68; 27
Annonaceae	*Xylopia frutescens*	0.75	1	Animal	Insect	Too Rare	79; 68; 19; 27; 43
Annonaceae	*Xylopia macrantha*	1.5	3.75	Animal	Insect	Generalist	79; 68; 19; 27; 43
Annonaceae	*Xylopia sericophylla*	1	1.2	Animal	Insect	Generalist	10; 76; 68; 19; 60; 27; 32; 43
Apocynaceae	*Aspidosperma myristicifolium*	3	10.5	Wind	Insect	Too Rare	68; 79; 60; 32; 68
Apocynaceae	*Aspidosperma spruceanum*	2.1	14	Wind	Insect	Generalist	10; 22; 68; 60; 32
Apocynaceae	*Lacmellea panamensis*	1.5	3	Animal	Insect	Generalist	10; 79; 68; 60; 32
Apocynaceae	*Rauvolfia sp1*	2.05	NA	Animal	Insect	Too Rare	14; 10; 43
Apocynaceae	*Stemmadenia donnell-smithii*	1.13	7.91	Animal	Insect	Too Rare	79; 10; 68; 32

Apocynaceae	*Tabernaemontana longipes*	1	3.5	Animal	Insect	OG Specialist	79; 68; 80; 14; 74; 19; 27
Aquifoliaceae	*Ilex skutchii*	0.6	0.3	Animal	Insect	Too Rare	14; 68; 74; 27; 5
Araliaceae	*Dendropanax arboreus*	0.7	0.7	Animal	Insect	Generalist	10; 60; 5; 34
Araliaceae	*Schefflera morototoni*	0.5	0.6	Animal	multiple	Too Rare	34; 79; 64; 43
Arecaceae	*Astrocaryum alatum*	3.5	5.4	Animal	Insect	Too Rare	79; 77; 72; 14; 19; 27
Arecaceae	*Astrocaryum standleyanum*	3	4	Animal	Insect	Generalist	79; 79; 34; 60; 27
Arecaceae	*Attalea butyraceae*	4.5	6.5	Animal	Insect	Too Rare	79; 23; 60; 32; 27
Arecaceae	*Bactris glandulosa*	1.8	1.05	Animal	Insect	Too Rare	79; 77; 80; 14; 27; 32
Arecaceae	*Euterpe precatoria*	0.7	1	Animal	Insect	Too Rare	10; 29, 76; 60; 27
Arecaceae	*Geonoma deversa*	0.62	0.7	Animal	Insect	Too Rare	10; 27
Arecaceae	*Iriartea deltoidea*	1.4	1.55	Animal	Insect	OG Specialist	79; 10; 29; 76; 13; 27; 5
Arecaceae	*Socratea exorrhiza*	2.2	3.25	Animal	Insect	OG Specialist	79; 10; 71;79; 60; 27; 5
Arecaceae	*Welfia regia*	3.0375	4	Animal	Insect	Too Rare	79; 10; 76; 27; 5
Bignoniaceae	*Amphitecna kennedyi*	1.4	14.5	Animal	Insect	Too Rare	10; 68; 32
Bignoniaceae	*Crescentia cujete*	0.75	21.5	Animal	Bat	Too Rare	68; 7
Bignoniaceae	*Jacaranda copaia*	0.5	11	Wind	Insect	Generalist	79; 38
Bignoniaceae	*Tabebuia chrysantha*	2.45	30.5	Wind	Insect	Too Rare	79; 77; 13; 60; 70
Boraginaceae	*Bourreria rinconensis*	NA	1.75	Animal	bat/insect	Too Rare	77; 27; 20
Boraginaceae	*Cordia bicolor*	1.5	1	Animal	Insect	SG Specialist	35; 79; 68; 60; 27; 32
Boraginaceae	*Cordia collococa*	0.5	0.71	Animal	Insect	Too Rare	68; 13; 80; 60; 14; 74; 27; 32
Boraginaceae	*Cordia cymosa*	0.6	1	Animal	Insect	Too Rare	79; 77; 80; 60; 14; 74; 27; 32
Boraginaceae	*Cordia megalantha*	0.9	1.15	Animal	Insect	Too Rare	68; 80; 14; 27; 32
Boraginaceae	*Cordia sp1*	0.95	NA	Animal	Insect	Too Rare	14; 27; 32
Burseraceae	*Protium aracouchini*	1.45	1.6	Animal	Insect	Too Rare	79; 80; 14; 4; 32; 68
Burseraceae	*Protium copal*	1.7	2.85	Animal	Insect	Too Rare	80; 60; 14; 74; 32
Burseraceae	*Protium costaricense*	1	NA	Animal	Insect	Too Rare	10; 79; 4; 32
Burseraceae	*Protium glabrum*	1.1	17.5	Animal	Insect	OG Specialist	79; 10; 76; 34; 4; 32
Burseraceae	*Protium mediano*	1.4	NA	Animal	Insect	Too Rare	14; 4; 32
Burseraceae	*Protium panamense*	1.75	2.8	Animal	Insect	Generalist	79; 35; 79; 32
Burseraceae	*Protium pecuniosum*	2.5	3	Animal	Insect	Generalist	79; 77; 4; 32
Burseraceae	*Protium pequeño*	1.4	NA	Animal	Insect	Too Rare	14; 4; 32
Burseraceae	*Protium ravenii*	2.5	2.75	Animal	Insect	OG Specialist	79; 75; 68; 60; 14; 74; 4; 32
Burseraceae	*Protium schippii*	1.5	2	Animal	Insect	OG Specialist	80; 14; 74; 4; 32
Burseraceae	*Protium sp1*	1.4	NA	Animal	Insect	Too Rare	14; 4; 32
Burseraceae	*Protium sp2*	1.4	NA	Animal	Insect	Too Rare	14; 4; 32
Burseraceae	*Protium sp3*	1.4	NA	Animal	Insect	Too Rare	14; 4; 32
Burseraceae	*Tetragastris panamensis*	1.75	2.75	Animal	Insect	OG Specialist	79; 79; 76; 10; 60; 4
Burseraceae	*Trattinnickia aspera*	1	1.1	Animal	Insect	Too Rare	79; 60; 4

Calophyllaceae	*Calophyllum brasiliense*	2.165	2.2	Animal	Insect	Too Rare	76; 19; 60; 41; 27; 32
Calophyllaceae	*Calophyllum longifolium*	2	3.5	Animal	Insect	Too Rare	79; 79; 69; 60; 32
Calophyllaceae	*Marila laxiflora*	0.08	4.75	Wind	Insect	OG Specialist	79; 79; 27; 69
Calophyllaceae	*Marila pluricostata*	0.05	2.5	Wind	Insect	Too Rare	69; 27
Cannabaceae	*Celtis schippii*	1	1.8	Animal	Wind	Too Rare	10; 79
Capparaceae	*Capparidastrum discolor*	0.05	13.5	animal	Insect	Too Rare	80; 68; 74; 32
Capparaceae	*Crateva tapia*	1	4.75	animal	Insect	Too Rare	77; 34; 80; 19; 60; 32; 34
Capparaceae	*Preslianthus pittieri*	1	6.5	NA	Insect	Too Rare	80; 68; 14; 32
Capparaceae	*Quadrella isthmensis*	1	NA	NA	Insect	OG Specialist	80; 14; 32
Caryocaraceae	*Anthodiscus chocoensis*	2.6	1.9	NA	Bat	Too Rare	34; 60; 14
Caryocaraceae	*Caryocar costaricense*	3.9	4	animal	Bat	OG Specialist	79; 23; 34; 60; 74; 41
Celastraceae	*Cheiloclinium cognatum*	1.05	3.5	animal	NA	OG Specialist	79; 23; 80; 14; 27
Celastraceae	*Crossopetalum parviflorum*	1	1.7	animal	NA	Too Rare	79; 69
Celastraceae	*Maytenus guyanensis*	0.94	1.5	animal	Insect	Too Rare	69; 75; 19; 32
Chrysobalanaceae	*Hirtella lemsii*	1.45	2.15	animal	Insect	Too Rare	10; 69; 75; 14; 32; 43
Chrysobalanaceae	*Hirtella racemosa*	1.2	1.7	animal	Insect	Too Rare	79; 69; 32; 43
Chrysobalanaceae	*Hirtella sp1*	1.45	NA	animal	Insect	Too Rare	14; 32; 43
Chrysobalanaceae	*Hirtella triandra*	1.7	2.35	animal	Insect	Too Rare	79; 32; 43
Chrysobalanaceae	*Licania operculipetala*	2.75	2.75	animal	Insect	Too Rare	75; 69; 60; 14; 32
Chrysobalanaceae	*Licania sparsipilis*	2.85	1.75	animal	Insect	Too Rare	79; 75; 69; 14; 32
Chrysobalanaceae	*Maranthes panamensis*	5	5	animal	NA	Too Rare	79; 10; 69, 79
Clusiaceae	*Chrysochlamys glauca*	1	1.5	animal	Insect	Too Rare	69; 27
Clusiaceae	*Chrysochlamys grandifolia*	1.5	4.25	animal	Insect	Too Rare	79; 77; 69; 27
Clusiaceae	*Chrysochlamys longifolium*	0.75	NA	animal	Insect	Too Rare	14; 27
Clusiaceae	*Chrysochlamys skutchii*	1	3.25	animal	Insect	Too Rare	69; 27
Clusiaceae	*Garcinia madruno*	2	4	animal	Insect	Generalist	79; 69; 77; 27; 32
Clusiaceae	*Garcinia spC*	2.85	1.65	animal	Insect	Too Rare	14; 79; 27; 32; 30
Clusiaceae	*Symphonia globulifera*	2.5	3.25	animal	Bird	OG Specialist	79; 10; 79; 76; 60; 27
Clusiaceae	*Tovomita longifolia*	2.5	4.25	animal	Insect	OG Specialist	79; 69; 27
Clusiaceae	*Tovomita stylosa*	1.5	2	animal	Insect	Too Rare	79; 69; 27
Combretaceae	*Terminalia amazonia*	0.6	1.4	Wind	Insect	SG Specialist	79; 69; 75; 60; 59; 5
Combretaceae	*Terminalia oblonga*	0.75	1.55	Wind	Insect	Too Rare	79; 72; 13; 60; 32
Convolvulaceae	*Dicranostyles ampla*	0.9	2.8	animal	Insect	Too Rare	75; 80; 74; 19; 59
Dichapetalaceae	*Dichapetalum nervatum*	5	1.9	animal	Insect	Too Rare	77; 5; 10; 30
Elaeocarpaceae	*Sloanea guapilensis*	2	1.5	animal	Insect	Too Rare	69; 80; 14; 74; 27; 32; 10
Elaeocarpaceae	*Sloanea guianensis*	1.5	2	animal	Insect	Too Rare	69; 75; 80; 14; 74; 19; 10
Elaeocarpaceae	*Sloanea sulcata*	2	5.1	animal	Insect	Too Rare	69; 60; 27; 32; 10
Elaeocarpaceae	*Sloanea zuliaensis*	1.3	2	animal	Insect	Too Rare	79; 69; 27; 32; 10
Erythroxylaceae	*Erythroxylum macrophyllum*	0.5	1	animal	Insect	Too Rare	10; 69; 75; 80; 14; 74; 27

Euphorbiaceae	*Acalypha diversifolia*	0.18	0.3	explosive	Insect	Too Rare	79; 35; 72; 69; 14; 27
Euphorbiaceae	*Alchornea costaricensis*	0.5	0.7	animal	Insect	SG Specialist	79; 32; 27
Euphorbiaceae	*Alchornea grandis*	0.4	0.8	animal	Insect	Too Rare	79; 14; 74; 27
Euphorbiaceae	*Alchornea latifolia*	0.85	0.75	animal	Insect	Too Rare	41; 69; 79; 60; 27; 30
Euphorbiaceae	*Alchorneopsis floribunda*	0.2	0.4	animal	Insect	Too Rare	10; 69; 27
Euphorbiaceae	*Croton schiedeanus*	0.8	1.1	explosive	Insect	Generalist	10; 69; 27; 32
Euphorbiaceae	*Croton smithianus*	1.8	0.8	explosive	Insect	SG Specialist	60; 14; 27; 32
Euphorbiaceae	*Mabea occidentalis*	0.53	1.9	explosive	multiple	OG Specialist	10; 69; 27; 4
Euphorbiaceae	*Pausandra trianae*	1	1.2	NA	Insect	OG Specialist	69; 60; 27; 30
Euphorbiaceae	*Pera arborea*	0.6	1.3	animal	multiple	Too Rare	69; 23; 14; 74; 79; 27; 43
Euphorbiaceae	*Sapium allenii*	0.4	0.8	animal	Insect	Too Rare	69; 14; 74; 27; 32
Euphorbiaceae	*Sapium glandulosum*	0.55	1.1	animal	Insect	Too Rare	79; 10; 69; 79; 32
Fabaceae	*Abarema adenophora*	1	3.25	animal	Insect	Too Rare	68; 60; 4; 30
Fabaceae	*Andira inermis*	2	3.5	animal	Insect	Too Rare	48, 13; 60; 4
Fabaceae	*Balizia elegans*	NA	14.5	animal	Insect	Too Rare	60; 34; 4; 10
Fabaceae	*Cassia grandis*	1.5	60	animal	Insect	Too Rare	79; 71; 32
Fabaceae	*Dialium guianense*	0.85	1.35	animal	Insect	OG Specialist	79; 34; 68; 77; 4
Fabaceae	*Diphysa americana*	0.6	7.5	Wind	Insect	Too Rare	79; 71; 13; 41; 4
Fabaceae	*Dussia macroprophyllata*	2.7	9.25	animal	Insect	Too Rare	75; 72; 60; 14; 4; 5
Fabaceae	*Dussia Mexicana*	2.75	4.5	animal	Insect	Too Rare	80; 14; 74; 4; 5
Fabaceae	*Enterolobium cyclocarpum*	1.75	11.5	animal	Insect	Too Rare	79; 71; 34; 60; 41; 4; 32
Fabaceae	*Fairchildia panamensis*	7.5	22	NA	Insect	Too Rare	77; 4; 30
Fabaceae	*Inga acrocephala*	1	18.5	animal	multiple	OG Specialist	79; 68; 60; 27; 32
Fabaceae	*Inga acuminate*	1	10	animal	multiple	Too Rare	10; 57; 68; 27; 32
Fabaceae	*Inga alba*	1.4	15.5	animal	multiple	Generalist	57; 27; 32
Fabaceae	*Inga bella*	1.25	20.75	animal	multiple	Too Rare	68; 60; 14; 27; 32
Fabaceae	*Inga coruscans*	1.9	22	animal	multiple	Too Rare	14; 34; 74; 27; 32
Fabaceae	*Inga jimenezii*	1.25	20.5	animal	multiple	Too Rare	14; 27; 32
Fabaceae	*Inga litoralis*	1.25	19	animal	multiple	Generalist	77; 68; 27; 32
Fabaceae	*Inga marginata*	1	10.75	animal	multiple	Too Rare	79, 57; 19; 27; 32
Fabaceae	*Inga multijuga*	1.5	17	animal	Insect	SG Specialist	79; 34; 60; 32
Fabaceae	*Inga nobilis*	1	10.5	animal	multiple	Too Rare	79; 80; 34; 14; 74; 27; 32
Fabaceae	*Inga oerstediana*	1.35	16	animal	multiple	Too Rare	14; 34; 74; 27; 32; 30
Fabaceae	*Inga polita*	0.75	9	animal	multiple	Too Rare	79; 68; 27; 32
Fabaceae	*Inga punctate*	1.3	14	animal	Insect	Too Rare	10; 79, 57; 79; 32
Fabaceae	*Inga sapindoides*	1.5	22	animal	multiple	Too Rare	79; 35; 79; 75; 60; 27; 32
Fabaceae	*Inga sp1*	1.25	NA	animal	multiple	Too Rare	10; 14; 27; 32
Fabaceae	*Inga sp2*	1.25	NA	animal	multiple	Too Rare	14; 27; 32
Fabaceae	*Inga spP10*	1.25	NA	animal	multiple	Too Rare	14; 27; 32

Fabaceae	*Inga spP8*	1.25	NA	animal	multiple	Too Rare	14; 27; 32
Fabaceae	*Inga thibaudiana*	1.25	12	animal	multiple	SG Specialist	79; 10; 79, 57; 60; 27; 32
Fabaceae	*Inga umbellifera*	1.75	11.5	animal	multiple	Too Rare	10; 79, 57; 27; 32
Fabaceae	*Inga venusta*	0.5	32	animal	multiple	Too Rare	79; 57; 76; 60; 27; 32
Fabaceae	*Lonchocarpus ferrugineus*	1.4	17	Wind	Insect	Too Rare	79; 34; 4; 32
Fabaceae	*Lonchocarpus heptaphyllus*	1.5	6.75	Wind	Insect	Too Rare	79; 34; 4
Fabaceae	*Lonchocarpus macrophyllus*	1.3	7	Wind	Insect	SG Specialist	79; 77; 68; 80; 60; 74; 4; 32
Fabaceae	*Lonchocarpus sp1*	1.5	NA	Wind	Insect	Too Rare	4; 32
Fabaceae	*Ormosia coccinea*	1	1.25	animal	Insect	Too Rare	34; 60; 32
Fabaceae	*Ormosia macrocalyx*	1.75	6.5	animal	Insect	Too Rare	10; 34; 4; 32
Fabaceae	*Peltogyne purpurea*	2	4	animal	Insect	Generalist	77; 34; 13; 79; 60; 4
Fabaceae	*Pseudopiptadenia suaveolens*	3	31.5	NA	Insect	Too Rare	80; 60; 14; 74; 4; 30
Fabaceae	*Pterocarpus violaceus*	2	7.5	Wind	Insect	Generalist	68; 80; 14; 79; 77; 4; 5
Fabaceae	*Schizolobium parahyba*	2.5	12	Wind	Insect	Too Rare	79; 71; 34; 13; 4
Fabaceae	*Senna papillosa*	0.4	30	gravity	Insect	Too Rare	76; 34; 32; 43
Fabaceae	*Swartzia ochnacea*	2	3.75	animal	Insect	Too Rare	80; 60; 14; 74; 79; 4; 32
Fabaceae	*Tachigali versicolor*	2	13	Wind	Insect	Generalist	79; 34; 60; 4
Fabaceae	*Vachellia allenii*	0.75	10	NA	Insect	Too Rare	77; 80; 34; 60; 4
Fabaceae	*Zygia cognate*	1.4	19	animal	Insect	Too Rare	68; 80; 14; 74; 27; 4
Humiriaceae	*Humiriastrum diguense*	2.1	2.35	animal	NA	Too Rare	31, 79; 76; 60
Humiriaceae	*Vantanea barbourii*	2.75	2.9	animal	NA	Generalist	79; 23; 60; 14; 41
Hypericaceae	*Vismia baccifera*	0.23	1.5	animal	Insect	SG Specialist	79; 10; 79; 69; 77
Hypericaceae	*Vismia macrophylla*	0.3	1.35	animal	Insect	Too Rare	35; 79; 69; 10; 30
Lacistemataceae	*Lacistema aggregatum*	0.5	1	animal	Insect	SG Specialist	10; 77; 32
Lacistemataceae	*Lozania pittieri*	0.2	0.4	animal	NA	Too Rare	79; 79; 74
Lamiaceae	*Aegiphila panamensis*	0.6	1.2	animal	Insect	Too Rare	79; 5
Lamiaceae	*Aegiphila sp1*	0.6	NA	animal	Insect	Too Rare	79; 5
Lamiaceae	*Callicarpa acuminata*	0.3	NA	animal	NA	SG Specialist	10; 76
Lamiaceae	*Vitex cooperi*	1	1.45	animal	Insect	Too Rare	10; 79; 68; 76; 34; 60; 32; 5
Lauraceae	*Aiouea obscura*	NA	2.5	animal	Insect	Too Rare	77; 27
Lauraceae	*Caryodaphnopsis burgeri*	NA	2	animal	Insect	Too Rare	79; 77; 60; 27
Lauraceae	*Cinnamomum chavarranianum*	1	1.7	animal	Insect	Too Rare	75; 80; 6; 79; 27
Lauraceae	*Cinnamomun sp1*	1	1.25	animal	Insect	Too Rare	6; 27; 31
Lauraceae	*Licaria misantlae*	NA	3	animal	Insect	OG Specialist	31; 75; 80; 27
Lauraceae	*Licaria pergamentacea*	NA	3	animal	Insect	Too Rare	27; 31
Lauraceae	*Licaria sp1*	NA	1.5	animal	Insect	Too Rare	27; 31
Lauraceae	*Nectandra membranacea*	0.5	0.9	animal	Insect	Too Rare	79; 10; 31; 27; 32
Lauraceae	*Nectandra salicifolia*	0.85	1.1	animal	Insect	Too Rare	80; 14; 74; 32; 27
Lauraceae	*Nectandra sp2*	1.5	NA	animal	Insect	Too Rare	14; 27; 32

Lauraceae	*Nectandra umbrosa*	1	1.4	animal	Insect	SG Specialist	79; 31; 27; 32
Lauraceae	*Ocotea leucoxylon*	0.7	1.25	animal	Insect	Too Rare	14; 74; 27; 32; 43
Lauraceae	*Ocotea mollifolia*	1.05	3.25	animal	Insect	Too Rare	10; 31; 27; 32; 43
Lauraceae	*Ocotea multiflora*	1.45	2	animal	Insect	Too Rare	77; 14; 27; 32; 43
Lauraceae	*Ocotea pullifolia*	1.45	3.5	animal	Insect	OG Specialist	14; 27; 32; 31; 43
Lauraceae	*Ocotea sp1*	1.45	1	animal	Insect	Too Rare	14; 27; 32; 31; 43
Lauraceae	*Ocotea sp2*	1.45	1.5	animal	Insect	Too Rare	14; 27; 32; 31; 43
Lauraceae	*Ocotea sp3*	1.45	2.2	animal	Insect	Too Rare	14; 27; 32; 31; 43
Lauraceae	*Ocotea sp4*	1.45	1	animal	Insect	Too Rare	14; 27; 32; 31; 43
Lauraceae	*Ocotea sp5*	1.45	NA	animal	Insect	Too Rare	14; 27; 32; 43
Lauraceae	*Ocotea sp6*	1.45	NA	animal	Insect	Too Rare	14; 27; 32; 43
Lauraceae	*Ocotea spA*	1.45	NA	animal	Insect	Too Rare	14; 27; 32; 43
Lauraceae	*Persea Americana*	5.08	13	animal	Insect	Too Rare	71; 79; 27
Lauraceae	*Pleurothyrium golfodulcensis*	1.6	1.9	animal	Insect	Too Rare	74 (genus range); 27
Lauraceae	*Pleurothyrium pauciflorum*	1.6	1.9	animal	Insect	Too Rare	74 (genus range); 27
Lauraceae	*Williamodendron glaucophyllum*	NA	2	animal	Insect	Too Rare	80; 60; 27; 31
Lecythidaceae	*Couratari guianensis*	2	13	Wind	Insect	Too Rare	79; 77; 60; 4
Lecythidaceae	*Eschweilera biflava*	3	4.5	animal	bat/insect	SG Specialist	77; 4; 30
Lecythidaceae	*Eschweilera collinsii*	3	9	animal	bat/insect	Too Rare	72; 4
Lecythidaceae	*Eschweilera neei*	1	2	animal	bat/insect	Too Rare	79; 60; 14; 32
Lecythidaceae	*Eschweilera panamensis*	4.05	NA	animal	bat/insect	Too Rare	79; 14; 4
Lecythidaceae	*Eschweilera sp2*	4.05	NA	animal	bat/insect	Too Rare	14; 4
Lecythidaceae	*Grias cauliflora*	3.75	6	animal	Insect	Too Rare	75; 72; 60; 4
Lecythidaceae	*Gustavia brachycarpa*	2.05	2.5	animal	Insect	OG Specialist	79; 80; 60; 14; 19; 4; 43
Lepidobotryaceae	*Ruptiliocarpon caracolito*	NA	3.25	animal	NA	Too Rare	79; 60
Magnoliaceae	*Talauma gloriensis*	1.3	12.5	animal	Insect	Too Rare	10; 72; 60; 27
Malpighiaceae	*Bunchosia macrophylla*	1.07	1.64	animal	Insect	Too Rare	10; 27; 32
Malpighiaceae	*Byrsonima crassifolia*	0.85	1.5	animal	Insect	Too Rare	71; 34; 79; 5
Malpighiaceae	*Byrsonima crispa*	0.8	1.25	animal	Insect	Too Rare	79; 10; 80; 60; 14; 74; 5
Malpighiaceae	*Malpighia albiflora*	0.5	1	animal	NA	Too Rare	79; 78; 80; 74
Malvaceae	*Apeiba membranacea*	0.4	5	animal	Insect	Too Rare	35; 60; 32; 5
Malvaceae	*Apeiba tibourbou*	0.5	6	animal	Insect	SG Specialist	79; 35; 71; 60; 32; 43
Malvaceae	*Bombacopsis sessilis*	1	10.5	Wind	bat/insect	Generalist	79; 60; 32
Malvaceae	*Ceiba pentandra*	0.5	18	Wind	Bat	Too Rare	10; 71; 14; 60; 5
Malvaceae	*Goethalsia meiantha*	1.5	3.5	Wind	Insect	SG Specialist	10; 75; 73; 60; 5
Malvaceae	*Guazuma ulmifolia*	0.3	2.75	animal	Insect	SG Specialist	79; 71; 73; 40; 60; 32; 43
Malvaceae	*Hampea appendiculata*	0.75	2.5	animal	Insect	Too Rare	79; 35; 60; 71; 32; 5
Malvaceae	*Heliocarpus appendiculatus*	0.2	1	Wind	Insect	Too Rare	71; 80; 14; 74; 79; 60; 5
Malvaceae	*Luehea seemannii*	0.85	2.75	Wind	bird/insect	SG Specialist	79; 35; 79; 13; 60; 32

Malvaceae	*Malvaviscus concinnus*	0.65	0.9	animal	bird/insect	Too Rare	79; 72; 80; 74; 27
Malvaceae	*Mortoniodendron cauliflorum*	NA	NA	animal	NA	Too Rare	77
Malvaceae	*Ochroma pyramidale*	0.4	17.5	Wind	Bat	Too Rare	79; 35; 71; 34; 60; 32
Malvaceae	*Pachira aquatic*	4	21.25	animal	Bat	Too Rare	10; 34; 60; 4; 5
Malvaceae	*Quararibea ochrocalyx*	1.1	3.85	animal	multiple	Too Rare	79; 68; 27; 32
Malvaceae	*Quararibea platyphylla*	1.75	2.55	animal	multiple	Too Rare	79; 68; 14; 19; 27; 32
Malvaceae	*Sterculia recordiana*	4.66	11	animal	Insect	Too Rare	79; 10; 75; 60; 32
Malvaceae	*Theobroma angustifolium*	3	14	animal	Insect	Too Rare	79; 60; 14; 74; 32; 4
Malvaceae	*Theobroma cacao*	2.5	17.5	animal	Insect	Too Rare	79; 79; 19; 4
Malvaceae	*Theobroma simiarum*	2.05	NA	animal	Insect	Too Rare	79; 80; 14; 4; 32
Malvaceae	*Trichospermum galeotii*	0.3	1.5	wind	NA	SG Specialist	79; 35; 60
Malvaceae	*Trichospermum grewifolium*	0.3	1.5	wind	NA	SG Specialist	60; 74
Melastomataceae	*Bellucia pentamera*	0.1	1.25	animal	Insect	Too Rare	79; 80; 14; 74; 27; 32
Melastomataceae	*Conostegia tenuifolia*	0.4	0.5	animal	Insect	Too Rare	79; 74; 53; 27
Melastomataceae	*Henriettea succosa*	0.7	1.3	animal	Insect	SG Specialist	79; 77; 80; 14; 74; 27
Melastomataceae	*Henriettea tuberculosa*	0.1	0.4	animal	Insect	OG Specialist	31; 75; 14; 27
Melastomataceae	*Miconia affinis*	0.25	0.45	animal	Insect	SG Specialist	79; 60; 27; 32; 5
Melastomataceae	*Miconia argentea*	0.1	0.4	animal	bird/insect	SG Specialist	79; 35; 14; 74; 32; 27
Melastomataceae	*Miconia elata*	0.1	0.5	animal	bird/insect	Too Rare	10; 79, 31; 27; 32
Melastomataceae	*Miconia hondurensis*	0.17	0.65	animal	bird/insect	Too Rare	79; 10; 27; 32; 31
Melastomataceae	*Miconia matthaei*	0.1	0.3	animal	bird/insect	Too Rare	79; 10; 14; 74; 27; 32
Melastomataceae	*Miconia multispicata*	0.06	0.32	animal	bird/insect	OG Specialist	31; 27; 32
Melastomataceae	*Miconia osaensis*	0.14	1	animal	bird/insect	Too Rare	77; 14; 27; 32
Melastomataceae	*Miconia poeppigii*	0.1	0.5	animal	bird/insect	Too Rare	14; 74; 27; 32
Melastomataceae	*Miconia prasina*	0.1	0.5	animal	bird/insect	Too Rare	14; 73; 74; 79; 27; 32
Melastomataceae	*Miconia schlimii*	0.05	0.5	animal	Insect	SG Specialist	79; 80; 14; 74; 32
Melastomataceae	*Miconia trinervia*	0.1	0.5	animal	bird/insect	SG Specialist	31; 27; 32
melastomataceae	*Mouriri cyphocarpa*	0.75	1.7	animal	bird/insect	Too Rare	79; 80; 60; 27; 32
Melastomataceae	*Mouriri gleasoniana*	0.83	1.25	animal	Insect	Too Rare	79; 10; 31; 60; 32
Meliaceae	*Carapa nicaraguensis*	5.1	7.5	animal	Insect	Generalist	10; 71; 76; 34; 13; 79; 60; 27
Meliaceae	*Cedrela odorata*	0.55	5.5	wind	Insect	Too Rare	14; 71; 34; 40; 60; 27
Meliaceae	*Guarea aguilarii*	1.25	4	animal	Insect	Too Rare	79; 14; 27; 32
Meliaceae	*Guarea bullata*	1.8	2.9	animal	Insect	OG Specialist	10; 75; 34; 27; 32
Meliaceae	*Guarea grandifolia*	1.5	4	animal	Insect	OG Specialist	10; 34; 13; 60; 27; 31
Meliaceae	*Guarea pterorhachis*	1.7	1.75	animal	Insect	Generalist	79; 75; 34; 80; 60; 14; 27; 32
Meliaceae	*Guarea sp1*	1.25	NA	animal	Insect	Too Rare	14; 27; 32
Meliaceae	*Guarea spP8*	1.25	NA	animal	Insect	Too Rare	14; 27; 32
Meliaceae	*Guarea spR*	1.25	NA	animal	Insect	Too Rare	14; 27; 32

Meliaceae	*Guarea tonduzii*	1	2.75	animal	insect	OG Specialist	79; 80; 34; 14; 74; 27; 32; 31
Meliaceae	*Guarea williamsii*	1.1	3.75	animal	insect	OG Specialist	80; 34; 14; 74; 60; 27; 32
Meliaceae	*Trichilia septentrionalis*	0.72	2.1	animal	insect	Too Rare	79; 10; 75; 34; 60; 27; 32
Meliaceae	*Trichilia spA*	0.7	NA	animal	insect	Too Rare	14; 27; 32
Meliaceae	*Trichilia spR*	0.7	NA	animal	insect	Too Rare	14; 27; 32
Meliaceae	*Trichilia tuberculata*	1.5	1.7	animal	insect	Too Rare	79; 35; 68; 60; 32; 27
Monimiaceae	*Mollinedia costaricensis*	0.7	1.05	animal	NA	Too Rare	10; 31; 75
Moraceae	*Batocarpus costaricensis*	1.85	7	animal	wind	OG Specialist	79; 77; 60; 14; 19; 32
Moraceae	*Brosimum alicastrum*	1	2	animal	insect	Too Rare	79; 71; 19; 60; 27; 32
Moraceae	*Brosimum costaricanum*	1.65	1.1	animal	insect	Too Rare	79; 77; 80; 60; 14; 27; 32
Moraceae	*Brosimum guianense*	1.4	1.5	animal	insect	Generalist	10; 79; 22; 60; 27; 32
Moraceae	*Brosimum lactescens*	1.2	3	animal	insect	Generalist	10; 76; 19; 60; 27; 32
Moraceae	*Brosimum utile*	3	2.75	animal	insect	Generalist	79; 79; 68; 60; 27; 32
Moraceae	*Castilla tunu*	0.1	2.75	animal	wind	Generalist	79; 77; 80; 60; 14; 74; 27
Moraceae	*Clarisia biflora*	0.5	2.5	animal	wind	Too Rare	10; 19; 60; 27
Moraceae	*Ficus bullenei*	0.2	1	animal	insect	Too Rare	14; 60; 74; 79; 5
Moraceae	*Ficus citrifolia*	0.05	1.1	animal	insect	Too Rare	79; 77; 73; 60; 5
Moraceae	*Ficus colubrinae*	0.1	0.6	animal	insect	Too Rare	14; 77; 74; 79; 5
Moraceae	*Ficus costaricana*	0.07	1	animal	insect	Too Rare	79; 77; 80; 60; 14; 73; 5
Moraceae	*Ficus insipida*	0.3	2.75	animal	insect	SG Specialist	79; 79; 60; 5
Moraceae	*Ficus maxima*	0.1	1.7	animal	insect	Generalist	77; 79; 60; 5
Moraceae	*Ficus moraziana*	0.2	2.05	animal	insect	Too Rare	14; 27; 32; 5; 31
Moraceae	*Ficus nymphaeifolia*	0.1	2.1	animal	insect	Too Rare	79; 60; 5
Moraceae	*Ficus obtusifolia*	0.1	2.05	animal	insect	Too Rare	79; 80; 60; 14; 74; 5
Moraceae	*Ficus osensis*	0.2	0.65	animal	insect	Too Rare	79; 14; 27; 32; 5; 31
Moraceae	*Ficus sp2*	0.2	NA	animal	insect	Too Rare	14; 27; 32; 5
Moraceae	*Ficus tonduzii*	0.6	1.3	animal	insect	Too Rare	10; 79; 79; 60; 5
Moraceae	*Ficus trachelosyce*	0.1	0.75	animal	insect	Too Rare	14; 74; 27; 32; 5
Moraceae	*Maclura tinctoria*	0.25	1.95	animal	wind	Too Rare	79; 41; 27
Moraceae	*Maquira costaricana*	1.5	2.5	animal	wind	Too Rare	79; 10; 60; 27
Moraceae	*Naucleopsis ulei*	1.25	6	animal	wind	OG Specialist	79; 80; 60; 14; 74; 27; 31
Moraceae	*Perebea hispidula*	0.7	2	animal	wind	Generalist	31; 76; 19; 60; 27
Moraceae	*Pseudolmedia spuria*	1	1.2	animal	insect	OG Specialist	79, 31 60; 14; 74; 19; 79; 32
Moraceae	*Sorocea affinis*	0.85	1.25	animal	wind	Too Rare	79; 77; 27; 70
Moraceae	*Sorocea pubivena*	0.75	1.25	animal	wind	OG Specialist	79; 10; 76; 77; 27; 70; 5
Moraceae	*Trophis racemosa*	0.5	0.65	animal	wind	Too Rare	79; 35; 79; 72; 60; 32
Myristicaceae	*Compsoneura excelsa*	3.5	3.7	animal	insect	OG Specialist	77; 4

Myristicaceae	*Otoba novogranatensis*	2.1	2.75	animal	Insect	Generalist	79; 60; 77; 4
Myristicaceae	*Virola koschnyi*	2.34	2.85	animal	bird/insect	Generalist	10; 71; 76; 13; 60; 32
Myristicaceae	*Virola macrocarpa*	3.5	4	animal	bird/insect	Generalist	79; 77; 4; 32
Myristicaceae	*Virola sebifera*	1.165	1.65	animal	Insect	Generalist	10; 76; 60; 32
Myristicaceae	*Virola spA*	1.6	2.45	animal	bird/insect	Too Rare	14; 4; 32; 31
Myristicaceae	*Virola surinamensis*	2.25	2.75	animal	bird/insect	OG Specialist	79; 60; 77; 4; 32
Myrtaceae	*Eugenia sp1*	2.1	NA	animal	Insect	Too Rare	14; 27; 32
Myrtaceae	*Eugenia sp2*	2.1	NA	animal	Insect	Too Rare	14; 27; 32
Myrtaceae	*Eugenia sp3*	2.1	NA	animal	Insect	Too Rare	14; 27; 32
Myrtaceae	*Myrcia sp2*	1.2	NA	animal	Insect	Too Rare	14; 27
Myrtaceae	*Myrcia splendens*	0.8	0.75	animal	Insect	Too Rare	10; 79, 31; 19; 60; 27
Myrtaceae	*Psidium guajava*	0.35	5	animal	Insect	SG Specialist	71; 31; 19; 27
Nyctaginaceae	*Guapira costaricana*	0.5	0.9	animal	multiple	Too Rare	79; 80; 74; 59
Nyctaginaceae	*Neea elegans*	1.25	1.27	animal	Insect	OG Specialist	79; 31; 75; 59; 32
Nyctaginaceae	*Neea psychotrioides*	0.7	0.8	animal	Insect	Too Rare	79; 10; 80; 14; 74; 59; 32
Nyctaginaceae	*Neea sp1*	1.2	NA	animal	Insect	Too Rare	14; 59; 32
Nyctaginaceae	*Neea sp2*	1.2	NA	animal	Insect	Too Rare	14; 59; 32
Nyctaginaceae	*Neea sp3*	1.2	NA	animal	Insect	Too Rare	14; 59; 32
Ochnaceae	*Ouratea rinconensis*	1.15	1.05	animal	Insect	Too Rare	14; 32; 31
Ochnaceae	*Quiina cruegeriana*	0.8	1.3	animal	NA	Too Rare	80; 14; 74; 10
Ochnaceae	*Quiina macrophylla*	0.78	1.3	animal	NA	Too Rare	75; 10
Olacaceae	*Chaunochiton kappleri*	0.8	10.5	wind	NA	Too Rare	80; 60; 14; 74
Olacaceae	*Heisteria acuminata*	1	1.75	animal	Insect	Generalist	79; 77; 32
Olacaceae	*Heisteria concinna*	1.25	5.9	animal	Insect	Generalist	10; 79; 60; 32; 31
Olacaceae	*Minquartia guianensis*	2.55	3.25	animal	Insect	Too Rare	31; 76; 41; 10
Passifloraceae	*Erblichia odorata*	NA	3.25	wind	NA	Too Rare	79; 80; 60
Phyllanthaceae	*Hieronyma alchorneoides*	0.25	0.35	animal	Insect	SG Specialist	10; 69; 13; 60; 32
Phyllanthaceae	*Margaritaria nobilis*	1	0.8	explosive	Insect	SG Specialist	79; 35; 27
Piperaceae	*Piper aduncum*	0.05	NA	animal	Insect	SG Specialist	80; 14; 74; 10
Piperaceae	*Piper aequale*	0.05	NA	animal	Insect	SG Specialist	80; 14; 74; 79; 10
Piperaceae	*Piper reticulatum*	0.1	NA	animal	Insect	Too Rare	79; 80; 14; 74; 10
Piperaceae	*Piper sp1*	0.22	NA	animal	Insect	Too Rare	14; 10
Piperaceae	*Piper sp2*	0.22	NA	animal	Insect	Too Rare	14; 10
Piperaceae	*Piper sp3*	0.22	NA	animal	Insect	Too Rare	14; 10
Polygonaceae	*Coccoloba obovata*	1	1.5	animal	Insect	Too Rare	79; 80; 14; 74; 19; 32
Polygonaceae	*Coccoloba sp1*	0.65	NA	animal	Insect	Too Rare	14; 19; 32
Polygonaceae	*Coccoloba sp2*	0.65	NA	animal	Insect	Too Rare	14; 19; 32
Polygonaceae	*Coccoloba standleyana*	0.65	0.7	animal	Insect	Too Rare	60; 14; 19; 32
Polygonaceae	*Coccoloba tuerckheimii*	1	1.04	animal	Insect	Too Rare	75; 14; 74; 19; 10; 32
Primulaceae	*Ardisia dodgei*	0.45	0.8	animal	Insect	Too Rare	80; 60; 14; 27; 32

Primulaceae	*Ardisia dunlapiana*	0.45	0.5	animal	insect	OG Specialist	80; 14; 77; 27; 32
Primulaceae	*Parathesis acostensis*	NA	5	animal	NA	Too Rare	80; 60
Proteaceae	*Roupala Montana*	1.5	3.25	wind	NA	Too Rare	60; 34; 79
Putranjivaceae	*Drypetes brownie*	1.2	2.5	animal	insect	OG Specialist	69; 74; 79; 27; 32
Rhizophoraceae	*Cassipourea elliptica*	0.5	0.85	animal	insect	Too Rare	79; 60; 14; 74; 5
Rubiaceae	*Arachnothryx bertieroides*	NA	NA	NA	insect	Too Rare	27
Rubiaceae	*Borojoa panamensis*	0.2	NA	animal	insect	Too Rare	10; 76; 27
Rubiaceae	*Borojoa patinoi*	0.62	9	animal	insect	Too Rare	79; 72; 10; 27
Rubiaceae	*Chimarrhis latifolia*	0.1	4.5	wind	insect	SG Specialist	79; 60; 15; 32; 27
Rubiaceae	*Chimarrhis parviflora*	0.1	0.2	animal	insect	SG Specialist	79; 15; 79; 27
Rubiaceae	*Chione silvestris*	1.1	1.3	animal	insect	Too Rare	74; 53; 27; 32
Rubiaceae	*Chomelia microloba*	0.9	1.5	animal	insect	Too Rare	79; 77; 80; 14; 74; 27; 32
Rubiaceae	*Chomelia venulosa*	1.15	NA	animal	insect	Too Rare	14; 79; 27; 32
Rubiaceae	*Condaminea corymbnosa*	1.2	1.4	NA	insect	Too Rare	74; 27
Rubiaceae	*Coussarea hondensis*	1	1.25	animal	insect	Too Rare	10; 75; 72; 80; 14; 74; 27; 5
Rubiaceae	*Coussarea nigrescens*	1.35	18	animal	insect	Too Rare	72; 80; 14; 27; 5
Rubiaceae	*Coussarea sp1*	1.35	NA	animal	insect	Too Rare	14; 27; 5
Rubiaceae	*Duroia costaricensis*	0.85	NA	NA	insect	Too Rare	14; 27
Rubiaceae	*Faramea sessifolia*	0.85	0.3	animal	insect	Too Rare	77; 80; 14; 27; 5
Rubiaceae	*Faramea suerrensis*	1	1.4	animal	insect	Too Rare	10; 75; 76; 80; 14; 74; 27; 32; 5
Rubiaceae	*Genipa Americana*	1	7.5	animal	bird/insect	Too Rare	79; 60; 32; 27; 32; 43
Rubiaceae	*Guettarda foliacea*	0.5	1.3	animal	insect	Too Rare	79; 75; 60; 74; 19; 27
Rubiaceae	*Guettarda macrosperma*	0.8	1.75	animal	insect	Too Rare	79; 74; 19; 27
Rubiaceae	*Guettarda samblasensis*	0.6	2.1	animal	insect	Too Rare	60; 19; 27
Rubiaceae	*Guettarda turrialbana*	0.6	2.6	animal	insect	Too Rare	77; 80; 19; 60; 27
Rubiaceae	*Hamelia magnifolia*	0.1	1.2	animal	bird	Too Rare	79; 14; 74; 19; 27
Rubiaceae	*Isertia laevis*	0.1	1.5	animal	insect	SG Specialist	79; 80; 60; 74; 27; 32
Rubiaceae	*Macrocnemum roseum*	0.2	1.4	wind	insect	Too Rare	79; 60; 14; 74; 27
Rubiaceae	*Palicourea guianensis*	0.95	1	animal	bird/insect	SG Specialist	79; 32; 27
Rubiaceae	*Pentagonia tinajita*	0.5	1.5	animal	insect	Too Rare	34; 80; 60; 14; 74; 79; 27
Rubiaceae	*Posoqueria latifolia*	1.25	5.5	animal	insect	Too Rare	79; 35; 79; 60; 32; 27
Rubiaceae	*Psychotria elata*	0.7	0.7	animal	bird	Too Rare	79; 10; 27; 5
Rubiaceae	*Psychotria grandis*	0.4	0.6	animal	insect	SG Specialist	35; 73; 79; 27
Rubiaceae	*Psychotria panamensis*	0.7	NA	animal	insect	Too Rare	10; 27
Rubiaceae	*Psychotria remota*	0.6	0.8	animal	insect	Too Rare	79; 80; 14; 74; 27
Rubiaceae	*Psychotria solitudinum*	0.5	0.5	animal	insect	Too Rare	14; 27
Rubiaceae	*Randia grandifolia*	0.7	3	animal	insect	Too Rare	10; 76; 77; 27; 5
Rubiaceae	*Randia sp1*	1.65	NA	animal	insect	Too Rare	14; 27; 5
Rubiaceae	*Tocoyena pittieri*	1.5	10	animal	insect	Too Rare	79; 60; 27

Rubiaceae	*Warszewiczia coccinea*	0.07	0.4	wind	bird/insect	SG Specialist	71; 79; 72; 60; 27; 5
Rutaceae	*Zanthoxylum acuminatum*	0.4	0.5	animal	Insect	Too Rare	79; 60; 14; 74; 27; 5
Rutaceae	*Zanthoxylum panamense*	0.4	0.7	animal	Insect	Too Rare	79; 10; 79; 27; 5
Sabiaceae	*Meliosma donnellsmithii*	1.45	NA	animal	Insect	Too Rare	14; 27; 5; 10
Sabiaceae	*Meliosma grandiflora*	1	2	animal	Insect	Too Rare	77; 27; 5; 10
Salicaceae	*Casearia arborea*	0.15	0.35	animal	multiple	SG Specialist	10; 79; 72; 60; 43
Salicaceae	*Casearia commersoniana*	0.45	0.7	animal	multiple	Too Rare	10; 79; 77; 43
Salicaceae	*Casearia sylvestris*	0.2	1	animal	multiple	SG Specialist	79; 10; 27; 43
Salicaceae	*Laetia procera*	0.27	2	animal	Insect	SG Specialist	79; 10; 79; 76; 74; 60; 5
Salicaceae	*Laetia spA*	NA	NA	animal	Insect	SG Specialist	79; 5
Salicaceae	*Lunania Mexicana*	0.15	0.5	animal	Insect	Too Rare	79; 80; 14; 74; 4
Salicaceae	*Pleuranthodendron lindenii*	0.5	0.85	NA	NA	Too Rare	79; 77; 75; 60
Salicaceae	*Tetrathylacium macrophyllum*	0.2	0.85	animal	Insect	SG Specialist	79; 23; 80; 60; 74; 4; 32
Sapindaceae	*Allophylus gentry*	1.05	1.15	wind	NA	Too Rare	79; 68; 14
Sapindaceae	*Cupania rufescens*	1	1.75	animal	Insect	SG Specialist	79; 19; 10; 27; 32
Sapindaceae	*Cupania sp1*	1.05	NA	animal	Insect	Too Rare	14; 19; 27; 32
Sapindaceae	*Dilodendron costaricense*	1.5	2.75	animal	Wind	Too Rare	79; 34; 80; 60; 74; 32
Sapindaceae	*Talisia allenii*	1.3	2.5	animal	Insect	Too Rare	79; 68; 32
Sapindaceae	*Talisia nervosa*	2	3	animal	Insect	Generalist	79; 10; 32
Sapindaceae	*Vouarana anomala*	1.25	2.75	animal	NA	Too Rare	68; 60; 10
Sapotaceae	*Chromolucuma rubriflora*	2.7	NA	NA	Insect	Too Rare	80; 14; 27
Sapotaceae	*Chrysophyllum argenteum*	1	5	animal	Insect	Too Rare	79; 19; 60; 27
Sapotaceae	*Chrysophyllum cainito*	1	7.5	animal	Insect	Too Rare	79; 13; 73; 19; 27
Sapotaceae	*Chrysophyllum sp1*	2.4	NA	animal	Insect	Too Rare	14; 19; 27
Sapotaceae	*Chrysophyllum sp2*	2.4	NA	animal	Insect	Too Rare	14; 19; 27
Sapotaceae	*Micropholis melinoniana*	NA	5.5	animal	Insect	Too Rare	79; 80; 60; 27
Sapotaceae	*Pouteria acuminata*	2.7	NA	animal	Insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria chiricana*	2.7	NA	animal	Insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria filipes*	2.7	4.75	animal	Insect	Too Rare	72; 80; 60; 14; 27; 32
Sapotaceae	*Pouteria fossicola*	3	9.5	animal	Insect	Too Rare	79; 71; 27
Sapotaceae	*Pouteria glomerata*	2.1	7.5	animal	Insect	Too Rare	14; 77; 60; 27; 32
Sapotaceae	*Pouteria juruana*	2.7	3.25	animal	Insect	OG Specialist	79; 60; 14; 27; 32
Sapotaceae	*Pouteria laevigata*	2.7	17.5	animal	Insect	OG Specialist	80; 60; 14; 27; 32
Sapotaceae	*Pouteria lecythidicarpa*	2.7	NA	animal	Insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria reticulate*	3	3	animal	Insect	Too Rare	79; 10; 76; 32
Sapotaceae	*Pouteria sp10*	2.7	NA	animal	Insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria sp2*	2.7	NA	animal	Insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria sp3*	2.7	NA	animal	Insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria sp4*	2.7	NA	animal	Insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria sp5*	2.7	NA	animal	Insect	Too Rare	14; 27; 32

Sapotaceae	*Pouteria sp6*	2.7	NA	animal	insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria sp7*	2.7	NA	animal	insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria sp8*	2.7	NA	animal	insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria spA*	2.7	NA	animal	insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria spC*	2.7	NA	animal	insect	Too Rare	14; 27; 32
Sapotaceae	*Pouteria subrotata*	1.75	2	animal	insect	Too Rare	14; 32
Sapotaceae	*Pouteria torta*	3.25	5	Animal	insect	OG Specialist	79; 10; 75; 72; 60; 27; 32
Sapotaceae	*Sarcaulus brasiliensis*	1.6	2	Animal	insect	Too Rare	79; 77; 27; 32
Simaroubaceae	*Simaba cedron*	4	8.25	Animal	insect	Generalist	79; 34; 80; 60; 14; 74; 32
Simaroubaceae	*Simaba polyphylla*	1.7	1.6	Animal	insect	Too Rare	79; 68; 80; 60; 14; 74; 4; 32
Simaroubaceae	*Simarouba amara*	1.3825	1.75	Animal	insect	Generalist	79; 79; 76; 72; 60; 4; 5
Siparunaceae	*Siparuna gesnerioides*	0.4	1.5	Animal	insect	SG Specialist	79; 80; 14; 74
Siparunaceae	*Siparuna guianensis*	0.5	1.25	Animal	insect	Generalist	79; 10; 80; 14; 74; 32
Siparunaceae	*Siparuna sp1*	0.45	4	Animal	insect	SG Specialist	14; 79
Solanaceae	*Cestrum megalophyllum*	0.42	0.64	Animal	insect	Too Rare	10; 75; 27; 5
Solanaceae	*Cestrum racemosum*	0.4	0.6	Animal	insect	Too Rare	10; 79; 73; 27; 5
Theaceae	*Gordonia brandegeei*	0.35	2.5	Wind	NA	Too Rare	74
Ulmaceae	*Ampelocera macrocarpa*	2	2.25	Animal	insect	OG Specialist	19; 60; 77; 10
Urticaceae	*Cecropia insignis*	0.2	25	Animal	wind	Generalist	71; 79; 27
Urticaceae	*Cecropia obtusifolia*	0.15	0.2	Animal	wind	Too Rare	18; 60; 27
Urticaceae	*Myriocarpa longipes*	0.1	0.2	Wind	NA	SG Specialist	79; 80; 74
Urticaceae	*Pourouma bicolor*	1.5	1.5	Animal	NA	OG Specialist	10; 79; 34
Urticaceae	*Urera baccifera*	0.3	0.5	Animal	wind	Too Rare	77; 71; 72; 19; 27
Violaceae	*Amphirrhox longifolia*	0.7	3	explosive	insect	OG Specialist	79; 80; 74; 43
Violaceae	*Gloeospermum diversipetalum*	0.85	NA	Animal	NA	Too Rare	14; 19
Violaceae	*Rinorea crenata*	0.8	1	Animal	insect	Too Rare	79; 80; 60; 14; 5
Violaceae	*Rinorea deflexiflora*	0.5	1.98	Animal	insect	Too Rare	10; 75; 5
Violaceae	*Rinorea hummelii*	0.7	2.75	Animal	insect	Too Rare	14; 74; 5
Violaceae	*Rinorea sp1*	0.8	NA	Animal	insect	Too Rare	14; 5
Violaceae	*Rinorea sylvatica*	0.4	2.5	explosive	insect	Too Rare	79; 5
Vochysiaceae	*Qualea polychroma*	3.9	NA	NA	insect	OG Specialist	76; 4
Vochysiaceae	*Vochysia allenii*	1	1.75	Wind	insect	Generalist	79; 60; 14; 4; 5
Vochysiaceae	*Vochysia ferruginea*	1	2.85	Wind	insect	SG Specialist	79; 79; 75; 13; 60; 4; 5
Vochysiaceae	*Vochysia guatemalensis*	2.85	4.5	Wind	insect	Too Rare	79; 75; 72; 60; 41; 4; 5

CHAPTER 2:

Remnant trees affect species composition but not structure of secondary forest

Introduction

Tropical forests are being destroyed at a rapid rate of ~64,000 km^2/yr. (Wright 2010), with 350 million hectares lost in the past century (Lamb *et al.* 2005). Following the abandonment of land formerly used for agriculture, pasture, or plantation, secondary forest is often able to regenerate quickly (Wright 2010), and with time, regenerating areas can approach the same level of ecosystem function and biodiversity as in nearby old growth forest (Lamb *et al.* 2005, Chazdon *et al.* 2009). Nearly half of the tropical forest remaining today is secondary or degraded forest (Wright and Muller-Landau 2006).

Remnant trees, old growth forest trees left on anthropogenically modified land, can potentially facilitate forest regeneration following pasture abandonment. Land owners across the tropics often leave remnant trees when they convert forests to pastures. Understanding the effects of remnant trees on forest regrowth can enhance management by helping determine the benefits of sparing individual trees when clearing forest and by serving as a proxy for evaluating ecological regeneration practices that rely on tree planting on recently abandoned land.

Remnant trees accelerate the regeneration of the forest after pasture abandonment through three processes: by facilitating seed dispersal into the pasture, by serving as seed sources, and by facilitating germination of seeds of forest species (i.e. Guevara *et al.* 1986, Manning *et al.* 2006, Nadkarni and Haber 2009). Through these processes, remnant trees serve as "regeneration nuclei" for secondary forest growth (McDonnell and Stiles 1983, Guevara *et al.* 1986). Current theories about remnant trees as regeneration nuclei and the underlying processes are largely based on studies conducted in currently active pasture or within a few years after pasture abandonment (Murray *et al.* 2008 but see Schlawin and Zahawi 2008). Further, most of these studies investigate effects of remnant trees on the structure and species richness of

regenerating forest, but do not evaluate effects on patterns of species abundance (i.e. Carriere *et al.* 2002, Carriere *et al.* 2002b, Schlawin and Zahawi 2008). Our study expands upon previous work by investigating effects of remnant trees on structure and composition of woody regeneration in 20-30 year old secondary forest. Studying the effects of remnant trees in older second growth forest allows us to make inferences about the longer-term effects of these trees on the regrowth of the surrounding forest. Our question is: How do remnant trees affect the structure, species composition, and diversity of regenerating tropical forest, 20-30 years following pasture abandonment? We also compare forest composition around remnant and reference trees with composition in survey plots in nearby second-growth (5-50 yr. old) and old growth forests.

Methods

Site Description

The study was conducted in lowland tropical humid forest (Holdridge *et al.* 1971) on the Osa Peninsula, Costa Rica, halfway between the town of Puerto Jiménez and Carate (the southern entrance to Corcovado National Park) by road. The flora of the Osa Peninsula is diverse with a high level of endemism (Aguilar *et al.* 2008); for example, it has at least 2142 plant species, representing over 185 families (Quesada *et al.* 1997), with more than 700 tree species as well as approximately 375 bird species, at least 220 species of breeding butterflies (excluding skippers, hairstreaks, and metalmarks), and 124 mammal species (Janzen1983, Barrantes *et al.* 1999). The mean annual temperature is 24-28˚C, and rainfall is 4.5-5.5 m/year (Herrera 1986, Kernan and Fowler 1995; Osa Conservation, pers. comm.). Most rain occurs during the wet season, April to November, with a peak in September and October (Osa Conservation, pers.

comm.). The dry season is December to March (Kernan and Fowler 1995; Osa Conservation, pers. comm.).

The study was conducted on land owned by Osa Conservation (OC, 8.41˚N, 83.34˚W) and Lapa Ríos Ecolodge and Wildlife Reserve (LR, 8.39˚N, 83.30˚W) within areas of 20-30 year old secondary forest (Figure 1). Elevation of the OC study sites is 37-76 m above sea level, with an average of 52 m. Most of this land is in the floodplain of the Piro River. Elevation of the LR study sites is 233-283 m above sea level, with an average of 254 m. The land at LR includes rolling hills, whereas the land at OC is fairly flat. Land at lower elevations generally receives less rainfall than at higher elevations on the Osa Peninsula. In 2010, the lowland Osa Conservation field station (35 m elevation) recorded a yearly total of about 4.8 m of rainfall whereas the upland Osa Conservation field station (300 m elevation) recorded a yearly total of about 5.5 m of rainfall. Slight temperature differences exist as well, with the lowland site recording in 2010 an average year temperature of 25.7˚C and the upland site recording an average year temperature of 22.2˚C (Osa Conservation, pers. comm.). Soils are primarily ultisols at both areas (Morales *et al.* 2012).

The second-growth forest sites are former cattle pastures. The land at LR was cleared in the late 1950s and used as pasture until 1991, when it was abandoned and allowed to regrow into forest. All of the OC land was cleared in the late 1960s, with the exception of the northeast portion near the Piro River, which was partially cleared in the late 1960s with further clearing between 1976 and 1980. All OC land was abandoned and began spontaneous natural regeneration in 1988. At the time of study, the secondary forest at LR was 20 years old with a historical pasture use of between 20 and 30 years. The secondary forest at OC was 23 years old with a historical pasture use of about 20 years. Land use history was verified with Osa

Conservation staff, with local landowners, and from aerial photographs from the Instituto Geográfico Nacional (San Jose, Costa Rica). The forest at both sites has closed canopies. Areas surrounding the study locations are primarily old growth or secondary forest, with a few large cleared tracts of pasture remaining to the west of the OC site and a few small areas of pasture to the south of the LR site (Figure 1).

Study Design

All surveys were conducted from May-July of 2011. We located 15 presumed remnant trees > 75 cm diameter at breast height (dbh) with no other large (>75 cm dbh) trees within 30 m, each at least 50 m from the nearest old growth forest edge (Fig. 1). Each identified remnant tree was paired with a nearby area of forest lacking remnant trees. One control tree in these forest areas lacking remnant trees was used as a center point for survey transects ("reference tree"). Reference trees were 50-150 m away from the paired remnant, had no trees > 75 cm dbh within 30 m, and were > 50 m away from the nearest old growth forest edge (Fig 1). Using nearby forest survey data of similarly aged secondary forest plots (Morales *et al.* 2012), we determined the height and dbh of trees in the 80^{th} percentile (from shortest to tallest and smallest to largest) to calculate acceptable height and dbh ranges for paired reference trees. Chosen reference trees were 16-35 m tall (mean 24.4 m) with a mean diameter at breast height (dbh) of 21-36.5 cm (mean 27.3 cm) (Table 1, calculated without trees later identified as emergents, see below). Remnant trees were considerably taller than remnants, at 42-55 m (mean 49.1 m) tall, with dbh of 113.0-201.5 cm (mean 144.3 cm) dbh (Table 1, calculated without trees later identified as emergents, see below). Remnant trees represented species generally found in old growth forest,

and were different species from the paired reference trees, which represented species generally found in second growth forest. Matching species of remnant and reference trees was not possible.

We used historical aerial photographs from the Instituto Geográfico Nacional from 1976, 1980, 1992, and 1995 to match GPS points taken in the field of the remnant trees to isolated trees in pasture. After careful examination of the historical photographs, five of the 15 presumed remnant trees were reclassified as emergent trees, as they were clearly not present in the old growth forest before clearing. Rather, these trees began growing around the time of pasture abandonment and quickly emerged as the tallest and largest trees in the re-growing forest. The 10 confirmed remnant trees represented 9 species and 8 families (Table 1). The 5 emergent trees represented 2 species and 2 families (Table 1). Heights of emergent trees were 38-51 m (mean 40.8 m) and diameters were 78.7-208.5 cm (mean 139.88 cm) (Table 1).

We measured height to the nearest meter for each remnant, emergent, and reference tree using a Haga altimeter. Three measurements were taken of each tree and averaged. If the tree had more than one stem at breast height, the dbh for all stems was measured and recorded. Crown radius was measured on the ground from the trunk of the tree to the greatest extent of the canopy along each transect. The four measurements were averaged and the radius of the tree bole was added to this average get the crown radius for each focal tree.

We placed four 5 m by 30 m transects at 90 degree angles to each other around each focal remnant, emergent, or reference tree. Transects were divided into six 5 m by 5 m quadrats. We measured all non-liana woody stems ≥ 1 cm dbh in the transects. Trees and treelets with multiple stems were counted as one individual. All measured stems ≥ 5 cm dbh were identified to species or morphospecies in the field. Treelets in genus *Piper* were identified to genus only (5.14% of all identified stems), owing to the difficulty of identification within this genus and the overall lack

of information about the *Piper* species found on the Osa Peninsula. Voucher specimens for some species, including those that we could not identify in the field, were collected and examined by Reinaldo Aguilar, the regional botanical expert (Vascular Plants of the Osa Peninsula, Costa Rica: http://sweetgum.nybg.org/osa/index.php, collecting permit Resolución No. 069-2011-SINAC, Sistema Nacional de Areas de Conservación). Dispersal vectors (wind, explosive, animal, water, gravity) for all woody species recorded in the study were determined from information found in the primary literature.

For a randomly selected subset of all remnant, emergent, and paired reference trees, we counted all free-standing, non-herbaceous seedlings > 30 cm in height and < 1 cm dbh in 1 m by 1 m square quadrats at the center of the quadrats 5 m and 10 m from the central tree in each four transects. Using a Skye red/far red (R:FR) light sensor and meter, we also took 3 measurements of R:FR ratio as an index of light availability. Measurements were taken in rapid succession in the center of each 1 m by 1 m square quadrat in which seedlings were counted, and they were taken under overcast to cloudy conditions at a height of 1 m (see Capers and Chazdon 2004).

Vegetation Structure and Diversity

We did not include the focal tree in calculations of density, basal area, or diversity or any analysis of the surrounding forest. Any quadrats with geographic barriers to regeneration, like streams or trails, were excluded from all calculations and analyses (13 quadrats excluded from remnant trees, 18 from reference trees, and no more than 4 quadrats excluded around a single central remnant or reference tree). In general, vegetation structure was calculated on an average per area basis (summed over all quadrats surveyed around a tree – all quadrats around a tree together are henceforth referred to as a "tree plot"), using all stems (for basal area) or all

individuals (for density) ≥ 1 cm dbh whereas local (alpha) diversity was calculated on a per tree basis, using all stems ≥ 5 cm dbh. Separate analyses were done for stems ≥ 5 and ≥ 10 cm dbh. Density was calculated by taking the sum of all trees found in a tree plot and dividing by the area surveyed. Basal area was calculated per stem by using the standard forestry formula (basal area (m^2) = $\pi*(\frac{dbh}{2})^2$) summed over one entire tree plot (generally 600 m^2) and divided by the total area in hectares. The 17 *Ficus* spp. trees found around remnant and reference trees could not be measured high enough on the trunk to exclude buttresses from the measured dbh. For this reason, the dbh measurement for these trees was multiplied by 0.65, the *Ficus* specific correction suggested by Glenday 2006, to get an improved (without buttress) dbh measurement that was then used to calculate basal area. Seedling density was calculated per tree as number of seedlings per unit area. Local diversity was calculated per tree as Shannon exponential diversity for stems ≥ 5 cm dbh and ≥ 10 cm dbh, using EstimateS (http://purl.oclc.org/estimates, Colwell 2012). Because some trees had fewer quadrats than others, Shannon exponential diversity at the greatest common number of quadrats was used for all trees. Shannon evenness (Shannon exponential diversity divided by richness) was calculated for all stems ≥ 5 cm dbh and ≥ 10 cm dbh with EstimateS. Species accumulation curves were also calculated in EstimateS, extrapolated to the greatest number of individuals in a single plot (Colwell et al 2012). Comparisons of species accumulation curves were made at 76 individuals for stems ≥ 5 cm dbh and 40 individuals for stems ≥ 10 cm dbh. Importance value indices were calculated for all species by the type of tree (remnant or reference) near which they were found. The index uses the sum of relative density, frequency, and basal area to rank species (Guariguata and Dupuy 1997, Guariguata *et al.* 1997).

We combined reference tree plots or remnant tree plots to calculate total (gamma) diversity, within group (alpha) diversity, and between group (multiplicative beta) diversity.

Because we had double the number of reference tree plots than remnant tree plots, we randomly subsampled 10 tree plots from all reference tree plots to use in the calculation of alpha and gamma diversity. This process was repeated 1000 times for both alpha and gamma diversity calculations, and we took the mean diversity of these 1000 iterations for each. All 10 remnant tree plots were combined for calculations of remnant tree diversity. Calculations were done for Hill numbers 0 (species richness), 1 (Shannon exponential diversity), and 2 (inverse Simpson diversity) for multiplicative alpha and beta diversity (where beta diversity equals gamma diversity divided by alpha diversity) presented by Jost *et al.* 2011.

Statistical Analysis

For the purposes of all analyses, the 5 emergent trees, which could not be considered remnant trees, were combined with the 15 reference trees to yield a total of 20 reference trees. All analyses were also performed as a paired design (as originally intended), with the 5 emergent trees and their paired reference trees discarded, but because none of the conclusions were different (all significance or non-significance was consistent), we report the non-paired results with 10 remnant trees and 20 reference trees.

To assess whether or not the presence of a remnant tree or the identity of its site affected basal area, tree density, local diversity, and species richness, we conducted two-way ANOVAs, using presence or absence of a remnant tree and site as random effects. Using site (LR or OC) as a random effect allowed us to eliminate the possibility that any differences found in the forest between remnant and reference trees were nothing more than site effects. For tree density models, the summed trees in all quadrats around a remnant or reference tree were standardized

by area of quadrats surveyed to account for the differences in survey area around the trees because of quadrats that had to be discarded. ANOVAs were run in R with the "stats" package.

We performed a power analysis to determine the magnitude of differences we could detect in basal area, seedling density, tree density, local diversity, or species richness, given our sample sizes. We randomly generated values from a normal distribution with specified means for remnant (10 values) and reference trees (20 values). We selected sets of means to determine the smallest possible difference in means for each measured or calculated value that could be detected with our sample sizes. Results of the power analyses are reported with ANOVA results.

We tested whether spatial autocorrelation was present in the data by creating semivariograms for basal area, tree density, and local diversity (gstat package in R: http://cran.r-project.org/web/packages/gstat/index.html). No evidence of spatial autocorrelation was found.

We used EstimateS to assess all pairwise similarities for species composition of the forest around remnant and reference trees. We calculated the pairwise distances with the Chao-Jaccard abundance-based estimator of similarity (Chao *et al.* 2005). Similarity between the forest around all of the remnant or reference trees and nearby old growth forests was calculated in the same way, using data from nearby forest survey plots (Morales *et al.* 2012). *Piper* spp. were not included in similarity or species ordination analyses because they were identified only to genus. Because the nearby forest survey plots were much larger than the remnant or reference tree plots (0.5 ha), they were separated into 10 discrete 500 m^2 subplots, each comprising five 10 m^2 quadrats. Pairwise similarities were calculated using all of these subplots. The pairwise similarities between the remnant tree plots, reference tree plots, and nearby forest subplots were plotted in non-metric multidimensional scaling (NMDS) space using the "vegan" package in R (http://cc.oulu.fi/~jarioksa/softhelp/vegan.html). For some analyses, the function "metaMDS" was

used to calculate pairwise distances and to plot pairwise similarities in NMDS space. In these cases, distance was specified as "chao", which returns Chao-Jaccard Abundance-based estimates of similarity comparable to EstimateS. To further assess whether or not the presence of a remnant tree or site affected pairwise similarity to old growth forest, we conducted two-way ANOVAs, using presence or absence of a remnant tree and site as random effects.

We ran an analysis of similarities (ANOSIM), also in the vegan package, to test whether or not the differences in species composition between forest around remnants and forest around references were statistically significant. As with the NMDS analysis, distance was specified as "chao." We also performed a linear regression analysis on the pairwise similarities between the forest around all of the remnant or reference trees and nearby old growth forest to determine if proximity to old growth forest was correlated with pairwise similarity. All remnant and reference trees were within 350 m of the edge of old growth forest (Fig. 1). We used an analysis of multinomial proportions with uninformative priors to compare the proportion of each dispersal mechanism around remnant trees and around reference trees using R2OpenBUGS in R (http://cran.r-project.org/web/packages/R2OpenBUGS/index.html) (McCarthy 2007).

Using a recently developed multinomial statistical method for classifying habitat specialists and generalists (see Chazdon *et al.* 2011 for full description of methods), we classified 278 species within the nearby eleven 0.5 ha forest survey chronosequence plots (Morales *et al.* 2012) into old growth specialists, second growth specialists, generalists, and too rare to classify. Morphospecies and *Piper* spp. were excluded from this analysis. The analysis was conducted using CLAM (Classification Method: http://chao.stat.nthu.edu.tw/softwareCE.html) with a *p*-level of 0.001 and a *k*-level of 0.667. We then applied these classifications to all species around remnant trees and to all species around reference trees. We used an analysis of multinomial

proportions with uninformative priors to determine the proportion of each category of trees around remnant and reference trees using R2OpenBUGS in R (McCarthy 2007).

Results

Structure of the regenerating forest

Forest surrounding remnant trees and reference trees did not differ significantly in terms of basal area, seedling density, or tree density. We found no effect of the presence of a remnant tree on basal area of the surrounding forest and no significant difference between the sites for stems ≥ 5 or ≥ 10 cm dbh (Table 2). Seedling density did not differ significantly between quadrats surrounding remnant or reference trees or between sites (Table 2). The presence of a remnant tree had no significant effect on the density of surrounding forest for all stems ≥ 1 cm dbh, but density was higher at OC than at LR (Table 2). However, this effect of site on density was not observed for stems ≥ 5 or ≥ 10 cm dbh (Table 2). Based on our power analysis and our sample sizes for remnant and reference trees, we would have been able to detect a difference of 1 m^2/ha for basal area, a difference of 1 seedling/m^2, and a difference of 0.75 trees/ha for density between remnant and reference tree plots. The red:far red ratio was not significantly different around the remnant trees sampled as compared with the reference trees sampled, nor was it significantly different between sites (Table 2, Table 3). We also found no relationship between seedling density and light ($F = 0.003$, $p = 0.960$, $R^2 < 0.001$).

Local richness and diversity of the regenerating forest

Extrapolated species richness for all stems ≥ 5 cm dbh was significantly greater surrounding the remnant trees than around reference trees, but not between sites (two-way

ANOVA, Table 2, Figure 2a). Extrapolated species richness did not different significantly in stems ≥ 10 cm dbh by the presence of a remnant tree or site (two-way ANOVA, Table 2, Figure 2b). Based on our power analysis, we would have been able to detect a difference of 1 species/individual for extrapolated species richness for all stems ≥ 5 cm dbh and a difference of 1.5 species/individual for extrapolated species richness for all stems ≥ 10 cm dbh. This significant difference in extrapolated richness for all stems ≥ 5 cm dbh but not for all stems ≥ 10 cm dbh indicates that stems 5.0-9.9 cm dbh, the relatively more recent recruits, are driving the significantly higher species richness surrounding remnant trees.

The presence of a remnant tree did not affect local (alpha) diversity as measured by Shannon exponential diversity, for stems ≥ 5 cm dbh or ≥ 10 cm dbh (Table 2). Site also had no effect on local diversity on either size class (Table 2). Shannon evenness was similar in the forests around all trees (range for all trees, all stems ≥ 5 cm dbh: 0.823-0.941). Species evenness was not significantly different between remnant and reference trees nor between sites (Table 2). Our power analysis showed that we would have been able to detect a difference in means of 1.5 for Shannon exponential diversity, and we would have been able to detect a difference in means of 0.5 for species evenness.

Species composition and beta diversity

A total of 170 species were found in the surveyed quadrats. We found a total of 118 species representing 42 families around 10 remnant trees (227 quadrats, each 25 m^2) and 129 species representing 42 families around 20 reference trees (461 quadrats, each 25 m^2). The most abundant species around remnant trees were *Socratea exorrhiza* (Arecaceae), *Chimarrhis latifolia* (Rubiaceae), *Piper* spp. (Piperaceae), *Tetrathylacium macrophyllum* (Flacourtiaceae),

Castilla tunu (Moraceae), and *Croton schiedeanus* (Euphorbiaceae), accounting for 33.5% of stems identified. The most abundant trees around reference trees were *Apeiba tibourbou* (Tiliaceae), *Luehea seemannii* (Tiliaceae), *Lacistema aggregatum* (Flacourtiaceae), *Piper* spp. (Piperaceae), *Spondias mombin* (Anacardiaceae), and *Castilla tunu* (Moraceae), accounting for 32.6% of stems identified. This ranking was similar, but not identical, to the species ranking using the importance value index (IVI, Table 4). Abundances of the top species around remnant and around reference trees were similar, with neither displaying a greater amount of dominance than the other. Using importance value, the top 10 species around reference trees show a greater dominance than the top 10 species around reference trees. This result arises largely from the fact that around reference trees, species of the highest density and frequency are the species with the greatest basal area. Remnant trees, by contrast, are associated with a few species of low density and frequency but very high basal area. Calculated within-group diversity (alpha diversity) was higher among remnants than among reference trees when all remnants and a subset of references were combined, respectively (Table 5). Between-group diversity (beta diversity), by contrast, was higher between reference trees than between remnant trees, for all remnants and a subset of references, respectively (Table 5).

Species composition around remnant trees was distinct from the species composition around reference trees; species were separated into two groups in NMDS space (stress=0.200, Figure 3). Using ANOSIM, we found that the species composition around the two tree types are significantly different for all stems ≥5 cm dbh (R=0.161, p=0.021). Including *Piper* spp. did not affect the significance of this result (R=0.150, p=0.044). ANOSIM further showed that the composition of stems ≥10 cm dbh was significantly different between remnant and reference trees (R=0.2618, p=0.003). When compared with the species composition of surrounding forest

of different ages, species composition of remnant forest and reference forest became part of a progression from early second-growth through late second-growth to old growth forest (Figure 4). Overall, species composition around remnants is more similar to that of old growth forest areas than it is to the species composition around reference trees (Figure 4).

Pairwise similarity was calculated between the forest around focal trees and nearby old growth forest within each study area (all stems ≥ 5 cm dbh). The pairwise similarity between remnant trees and old growth forest was significantly greater than the pairwise similarity between old growth forest and the forest around reference trees ($F = 193.0$, $p < 0.001$, $df = 1$) (Figure 5). Pairwise similarity was not correlated with distance to nearest old growth forest over all tree plots ($R^2 = 0.059$, $p = 0.196$), for plots grouped by site (for OC: $R^2 = 0.068$, $p = 0.347$; for LR: $R^2 = 0.013$, $p = 0.685$), or for plots grouped by remnant or reference trees (for reference trees: $R^2 = 0.020$, $p = 0.549$; for remnant trees: $R^2 = 0.049$, $p = 0.538$). Grouping by a larger size class (≥ 10 cm dbh) did not change this result.

Dispersal Mechanisms

Nearly 88% of the species found in the plots were animal-dispersed, 10.3% were wind-dispersed, and 1.7% used other dispersal mechanisms such as explosion and gravity (not accounting for abundance) (Appendix 1). Eighty-one percent of individuals ≥ 5 cm dbh around remnant trees were animal-dispersed, 13.88% were wind-dispersed, and 5.02% had other dispersal methods (based on abundance, Appendix 1, Table 6). In comparison, 82.86% of individuals ≥ 5 cm dbh around reference trees were animal-dispersed, 14.55% were wind-dispersed, and 2.59% had other dispersal methods (based on abundance, Appendix 1, Table 6). We found no significant differences in the proportion of animal-dispersed species or wind-

dispersed species around remnant trees, compared with the proportion around reference trees (Table 6).

Generalists and Specialists

Our classification method, with highly conservative p- and k-levels, assigned 15 species to the Old Growth Specialist ("OG Specialist") category, 21 species to the Secondary Growth Specialist ("SG Specialist") category, 20 species to the "Generalist" category, and 222 species to the Too Rare to Classify ("Rare") category (Table 7). All of these species were found in nearby forest survey plots that are part of a larger chronosequence study on the Osa Peninsula (Morales *et al.* 2012). Classifications assigned within the chronosequence data were applied to species found by our surveys around remnant and reference trees. Most species in our survey, excluding morphospecies and *Piper* spp., were present in the chronosequence survey and could be classified. (Inclusion of *Piper* spp., classified as either Rare or as SG Specialist, does not noticeably affect the proportions of each classification type around remnant or reference trees for stems ≥ 5 cm dbh. We found only 2 *Piper* spp. stems ≥ 10 cm dbh.) Of the classified species, 10 OG Specialist species, 20 SG specialist species, and 18 Generalist species were found in our survey (Table 7). Thirty-eight of the 162 species found in our survey were not found in the chronosequence survey. The overall abundances of these unclassified species were low; the highest abundance was 7 stems over all quadrats, and most species only occurred once in all of our quadrats. In the classification analysis, a species had to have an abundance of at least 10 stems to be classified into a group other than Rare. Therefore, all species found in our survey, but not in the chronosequence survey, were classified as Rare.

We observed significantly larger proportions of OG Specialist and Generalist trees around remnant trees than around reference trees (Figure 6a, Table 8). None of these additional OG Specialist or Generalist species around remnant trees were offspring of the remnant tree; only the remnant *Coccoloba tuerckheimii* had a conspecific tree around it, but *Coccoloba tuerckheimii* was classified as Rare. We also observed a significantly larger proportion of SG Specialist trees around reference trees compared to remnant trees (Figure 6a, Table 8). Similar trends in OG Specialists, Generalists, and SG Specialists are seen when the data are partitioned by site. For all stems ≥ 10 cm dbh, significantly more OG specialists around remnant trees and significantly more SG specialists were found around reference trees (Figure 6b, Table 8).

To determine whether the significant differences in OG Specialists and SG Specialists between the forest around remnants vs. references were due to abundance, we reduced the ≥ 5 cm and ≥ 10 cm dbh abundance data to incidence data. The forest around reference trees had a few SG Specialist species that were not found around remnants (*Miconia argentea*, *Palicourea guianensis*, *Trichospermum galeottii*, ≥ 5 cm dbh stem set), and the forest around remnant trees had a few OG Specialist species that were not found around references (*Cheiloclinium cognatum*, *Guarea williamsii*, *Gustavia brachycarpa*, *Pseudolmedia spuria*, ≥ 5 cm dbh stem set). Despite these slightly different sets of species between remnant trees and reference trees, we found no significant differences in the proportion of species of OG Specialists or SG Specialists around remnants and references. The lack of significant difference in proportions indicates that abundance of OG specialists and SG specialists and not presence or absence of species is largely driving the significant differences in specialists found between remnant and reference trees.

Discussion

Our study is the first to demonstrate that remnant trees have a lasting effect on the species composition of the surrounding regenerating forest, even 20-30 years after land abandonment, but no detectable effect on structural regeneration. Remnant trees in our 20-30 year old secondary forest did not significantly affect the basal area, tree or seedling density of surrounding regenerating forest as compared to reference trees in our study. Other studies have demonstrated that in the early years of regeneration, remnant or isolated pasture trees significantly impact regeneration through enhanced seed dispersal, seed germination, and seedling growth. Seeds are deposited in greater numbers and with greater species richness under remnant trees than 10 m away and further from the edge of the crown of the remnant (Slocum and Horvitz 2000, Elmqvist *et al.* 2001, Carriere *et al.* 2002, Schlawin and Zahawi 2008). Remnant trees may also serve as seed sources for the regenerating forest by dispersing their own seeds directly beneath the crown (Slocum and Horvitz 2000, Slocum 2001), although this was not found to be a significant regenerative factor in our study. Galindo-Gonzalez *et al.* (2000) postulate that remnant trees serve as "nurse plants" for newly dispersed seeds and recently germinated seedlings. Changes in levels of irradiance, air temperature, and soil moisture beneath crowns of remnant trees may affect seed germination and seedling growth, apart from effects on seed dispersal (Manning *et al.* 2006). Enhanced seed dispersal and enhanced seed germination contribute to enhanced seedling growth. Saplings and trees have higher density under the canopy of remnant trees than beyond the canopy edge (Elmqvist *et al.* 2001, Schlawin and Zahawi 2008). After regeneration begins, basal area is higher around remnant trees than in areas lacking remnant trees (Carriere et al 2002b, Schlawin and Zahawi 2008).

The results of the above studies have informed how we think about remnant trees and their effect on structural regeneration of tropical forest. With the exception of Schlawin and Zahawi (2008) who surveyed the regrowth around remnant trees in land 23 years past abandonment, all prior studies were conducted within a few years after land abandonment. We hypothesize that regeneration of our 20-30 year old secondary forests was sufficiently advanced that the forest structure had converged, erasing any potential earlier signal of enhanced regeneration in the forest around our remnant trees. Red:far red readings support the hypothesis that light conditions were fairly uniform in the second growth forest areas, regardless of remnant or reference tree. Further, we found no relationship between light conditions and seedling density among quadrats. Future studies of the mechanisms behind the enhanced regeneration around remnant trees would be beneficial to our understanding of the interplay between remnant trees and forest succession.

Changes in forest structure are only part of the regeneration process. All measures of species composition used in our study, with the exception of local (alpha) diversity (as measured by Shannon exponential diversity) and Shannon evenness, were affected by the presence of a remnant tree. We observed higher extrapolated species richness around remnant trees than in the other parts of the secondary forest. Moreover, tree assemblages around remnant trees are enriched with old growth and generalist species compared to other areas within the same secondary forest. This greater proportion of old growth and generalist species around remnant trees increases the similarity of species composition of forest around remnant trees to nearby old growth forest. While differences in stem density or basal area between forest around remnant trees and the rest of the secondary forest 20-30 years past abandonment were not found in our study, we have shown that remnant trees enrich forest regeneration in terms of species

composition. Studies that focus on remnant trees in later stages of forest growth, beyond 30 years past pasture abandonment, would show whether or not this effect of remnant trees on species composition continues.

Even after 20-30 years, remnant trees enrich forest regeneration either by enhancing dispersal of seeds or by facilitating the establishment, growth, or survival of dispersed seeds. In our extrapolated species richness analysis, the 5.0-9.9 cm size class was driving the difference between remnant and reference trees, indicating that the current impact of remnant trees on species composition reflects recent establishment events rather than initial post abandonment events, which have been erased by subsequent changes. Although we did not assess species composition in smaller size classes, this pattern would likely continue or be even greater for stems 1.0-4.9 cm dbh. We only found a few presumed offspring of the remnant trees in the 1.0-4.9 cm dbh size class per remnant tree (M. Sandor, pers. obs.), indicating that the offspring of the remnant trees are not contributing much to the species composition found around these trees. Remnant trees are associated with a greater abundance of OG Specialist species in the smaller size classes (5.0-19.9 cm dbh) than are reference trees, suggesting that, at least recently, remnant trees facilitated enhanced recruitment of OG Specialists and Generalists.

Composition of focal tree assemblages differed slightly between the two study areas. Because the two study areas differed somewhat in elevation, mean temperature, rainfall, and topography, these species differences between the sites are unexpected but not surprising. Generally, when a significant difference was found between remnant and reference trees, the degree of difference depended upon whether the sites were pooled or separated. This result indicates that, whereas some variations in the species participating exist at the site level, the

mechanisms that cause these differences between forest around remnant trees and forest around reference trees are operating at both sites.

Like remnant trees, early colonizing, rapidly growing trees can also play an important role in enhancing local regeneration by attracting seed dispersing frugivores in later stages of succession. Three of our individual emergent trees were *Ficus insipida*; *Ficus* spp. are common as isolated pasture trees in the active pastures near the LR site (M. Sandor, pers. obs.). Other studies have used the term "isolated trees" in pasture to show the same effects as have been seen with remnant trees (e.g. Guevara *et al.* 1992, Guevara and Laborde 1993, Galindo-Gonzalez *et al.* 2000, Slocum and Horvitz 2000, Slocum 2001, Guevara *et al.* 2004), but focusing on isolated trees allows inclusion of trees that recruit after the forest is cut for pasture (for example, trees with seedlings that cows do not like to eat), trees that are planted by the landholder for use (like fruit, fodder, or timber trees), and living fences (Harvey *et al.* 2011). Studies that look at the differences – and similarities – in function between emergent trees and remnant trees could inform the management of pasture sites in the tropics, both in what and how many trees are left when a site is cleared and in the decisions made about enhanced regeneration.

Landscape effects potentially play a large role in forest regeneration. A greater proportion of old growth forest in the landscape increases the regeneration capacity of abandoned pastures (Holl 1999, Chazdon 2003). Proximity to old growth forest could also affect regeneration around a remnant tree or in open pasture, although neither our study nor Laborde et al (2008) found any significant relationship. Remnant trees could mitigate edge effects by providing "stepping stones" in the landscape for seed dispersers (Guevara and Laborde 1993, Fischer and Lindenmayer 2002). Further, remnant trees often occur in patches (tree "islands") (Holl et al 2011). Seeds dispersed under remnant trees may come largely from other pasture trees or from

these tree islands instead of from nearby forest (Guevara and Laborde 1993, Slocum and Horvitz 2000, Slocum 2001), indicating that the amount of other remnants, isolated trees, or tree islands within the vicinity may also affect regeneration around a particular remnant. The presence of other remnant or isolated trees in the vicinity could explain why we found no relationship between pairwise similarity to and physical distance to old growth forest, even in the reference forest. Both of these factors, the effects of proximity to old growth forest and of nearby remnant or isolated trees or islands on the regeneration of forest, argue for a need to incorporate landscape factors such as area and proximity of old growth forest as well as presence of other remnant or isolated trees into future studies of forest regeneration.

Remnant and isolated pasture trees can be integral components of forest restoration strategies. They may help conserve animal diversity by providing an additional source of food in the landscape matrix or by providing breeding sites for native birds (Harvey et al 2006, Sekercioglu et al 2007) or roosts for bat species (M.R. Willig, pers. comm.). They also may enhance tree gene flow between across the landscape and therefore enhance genetic diversity (White et al 2002). Additionally, secondary forests, whether or not remnant trees are present, can be important for species conservation by fostering the establishment and growth of rare species. In our survey, 38 out of the 162 species we found (nearly 25% of all species found) over both remnant and reference tree plots were not present in the eleven 0.5 ha chronosequence plots nearby. All of these species were rare, with fewer than 7 individuals found in all of our quadrats. While the importance of conserving old growth forests is indisputable, secondary forests represent a reservoir of an additional set of rare species worth conserving (Chazdon et al 2009).

One method of managing abandoned tropical land is with enhanced regeneration, a process by which trees are planted in regenerating areas (or as tree islands) to help facilitate

regeneration (Aide et al 2000, Martinez-Garza and Howe 2003, Chazdon 2008, Cole *et al.* 2010). During the first few years after pasture abandonment, remnant trees accelerate the dispersal, establishment, and growth of seeds and seedlings. Eventually, the regrowth of the forest on abandoned open pasture converges structurally with that around the remnant trees, but remnant trees can continue to enhance the dispersal, establishment, and growth of seeds and seedlings of species typical of old growth forests for decades, assuming that old growth forest fragments and seed dispersing fauna remain in the landscape. Eventually the species composition of the surrounding forest, as well as the forest around the remnant trees, converge with nearby old growth stands. If remnant trees are left when land is cleared for anthropogenic uses, our study and a wealth of other studies demonstrate that, given a sufficient area of old growth forest in the landscape, assisted regeneration may not be necessary because abandoned pasture will eventually regenerate into forest similar to that of nearby old growth forests (Holl et al 2009). Further study of emergent and remnant trees in older secondary forest and in a variety of landscapes would help inform whether or not assisted regeneration is an effective strategy in highly degraded landscapes or on heavily used land. The results of these studies could also inform any cost/benefit analyses undertaken to determine which conservation actions, including assisted regeneration, are the most effective in particular landscapes.

Tables

Table 1. List of remnant, emergent, and reference trees. DBHs for all trees were measured as high as we could reach on the trunk, but we had no way to measure above the buttresses. DBHs were not corrected for buttresses. When a tree had two stems below breast height, the DBH of the largest stem is logged in the first DBH column and the DBH of the smallest stem is logged in the "2nd stem" column. Average distance from nearest old growth forest for reference trees was 129.25 m and for remnant trees was 99.5 m.

Genus	Species	Family	DBH (cm)	2nd stem (DBH)	Ht (m)	Canopy radius (m)	Distance to Nearest Old Growth Forest (m)	Elev (m)	Dispersal Mechanism of Focal Tree	OC or LR	Remnant, Emergent, or Reference	Classification
Apeiba	*tibourbou*	Tiliaceae	23.6	---	17	3.5	215	43.9	animal	OC	Reference	SG Specialist
Cordia	*bicolor*	Boraginaceae	36.5	13.6	29	5.6	60	54.6	animal	OC	Reference	SG Specialist
Cordia	*bicolor*	Boraginaceae	29.2	---	27	4.0	140	233.5	animal	LR	Reference	SG Specialist
Goethalsia	*meiantha*	Tiliaceae	31.5	---	25	3.1	50	61.6	wind	OC	Reference	SG Specialist
Hieronyma	*alchorneoides*	Euphorbiaceae	29.3	---	30	7.7	90	36.6	animal	OC	Reference	SG Specialist
Hieronyma	*alchorneoides*	Euphorbiaceae	31.5	---	24	5.0	115	246.6	animal	LR	Reference	SG Specialist
Hieronyma	*alchorneoides*	Euphorbiaceae	35.5	---	34	4.6	100	239.3	animal	LR	Reference	SG Specialist
Inga	*punctata*	Fabaceae	24.9	---	24	2.4	295	56.4	animal	OC	Reference	Too Rare
Inga	*multijuga*	Fabaceae	23.5	---	25	3.5	150	44.2	animal	OC	Reference	SG Specialist
Pourouma	*bicolor*	Cecropiaceae	25.2	3.7	19	3.7	100	245.7	animal	LR	Reference	OG Specialist
Spondias	*mombin*	Anacardiaceae	23.5	---	35	3.3	65	45.4	animal	OC	Reference	SG Specialist
Tabebuia	*chrysantha*	Bignoniaceae	21.7	---	20	2.2	55	52.7	wind	OC	Reference	Too Rare
Virola	*sebifera*	Myristicaceae	21.1	---	16	4.6	95	242.0	animal	LR	Reference	Generalist
Vochysia	*ferruginea*	Vochysiaceae	26.0	---	17	4.5	120	263.4	wind	LR	Reference	SG Specialist
Vochysia	*ferruginea*	Vochysiaceae	26.8	---	24	3.8	50	259.1	wind	LR	Reference	SG Specialist
Ficus	*insipida*	Moraceae	170.5	74.7	42	12.9	190	43.9	animal	OC	Emergent	SG Specialist
Ficus	*insipida*	Moraceae	208.5	---	51	16.6	315	44.8	animal	OC	Emergent	SG Specialist
Ficus	*insipida*	Moraceae	156.0	---	38	10.5	100	50.6	animal	OC	Emergent	SG Specialist
Spondias	*mombin*	Anacardiaceae	78.7	---	33	9.5	60	76.2	animal	OC	Emergent	SG Specialist
Spondias	*mombin*	Anacardiaceae	85.7	---	40	9.9	220	39.3	animal	OC	Emergent	SG Specialist
Caryocar	*costaricense*	Caryocaraceae	120.2	---	53	11.5	70	63.4	animal, gravity	OC	Remnant	Too Rare
Caryocar	*costaricense*	Caryocaraceae	201.5	---	55	16.0	145	257.9	animal, gravity	LR	Remnant	Too Rare
Coccoloba	*tuerckheimii*	Polygonaceae	117.0	3.9	42	8.6	100	257.0	animal	LR	Remnant	Too Rare
Ficus	*insipida*	Moraceae	172.5	---	42	14.3	155	283.5	animal	LR	Remnant	SG Specialist
Hieronyma	*alchorneoides*	Euphorbiaceae	124.5	---	51	13.0	65	54.3	animal	OC	Remnant	SG Specialist
Pouteria	*juruana*	Sapotaceae	136.5	---	55	7.4	50	258.2	animal	LR	Remnant	Too Rare
Pouteria	sp.	Sapotaceae	163.5	---	48	5.9	140	271.0	animal	LR	Remnant	Too Rare
Spondias	*mombin*	Anacardiaceae	131.4	---	37	11.0	140	247.5	animal	LR	Remnant	SG Specialist
Tachigali	*versicolor*	Fabaceae	113.0	---	55	14.2	75	58.5	animal, gravity	OC	Remnant	Too Rare
Terminalia	*oblonga*	Combretaceae	163.0	---	53	13.3	55	251.8	wind	LR	Remnant	Too Rare

Table 2. ANOVA results are shown for various measures of structure and diversity. Results with significant p-values are shown in bold, with a star next to the p-value.

	presence of remnant tree			**site**		
	F	**p**	**df**	**F**	**p**	**df**
basal area ≥1 cm dbh	0.182	0.673	1.000	0.790	0.382	1.000
basal area ≥5 cm dbh	0.167	0.686	1.000	0.701	0.410	1.000
basal area ≥10 cm dbh	0.221	0.642	1.000	0.977	0.332	1.000
seedling density	0.006	0.942	1.000	0.228	0.641	1.000
density ≥1 cm dbh	2.735	0.110	1.000	**11.062**	**0.003***	**1.000**
density ≥5 cm dbh	0.915	0.342	1.000	3.606	0.068	1.000
density ≥10 cm dbh	0.001	0.982	1.000	0.415	0.525	1.000
light	1.732	0.211	1.000	0.000	0.998	1.000
rarefied species richness ≥5 cm dbh	**20.964**	**<0.0001***	**1.000**	1.242	0.275	1.000
rarefied species richness ≥10 cm dbh	4.091	0.053	1.000	0.628	0.435	1.000
alpha diversity ≥5 cm dbh	0.242	0.627	1.000	0.421	0.522	1.000
alpha diversity ≥10 cm dbh	1.203	0.282	1.000	2.090	0.160	1.000
Shannon evenness ≥5 cm dbh	0.070	0.794	1.000	0.098	0.757	1.000
Shannon evenness ≥10 cm dbh	0.995	0.327	1.000	0.029	0.867	1.000

Table 3. Light data for all focal trees censused where light was measured. Averages are of the R:FR ratio and were obtained by averaging the eight 1 m^2 plots around the focal tree. Standard deviations are calculated based on sample.

Genus	Species	Family	Ref/Rem	Site	Light (R:FR) Mean	Light (R:FR) sd
Caryocar	*Costaricense*	Caryocaraceae	Rem	OC	0.731	0.100
Ficus	*Insipida*	Moraceae	Rem	LR	0.761	0.080
Pouteria	*Juruana*	Sapotaceae	Rem	LR	0.658	0.076
Pouteria	*sp.*	Sapotaceae	Rem	LR	0.755	0.112
Spondias	*Mombin*	Anacardiaceae	Rem	LR	0.686	0.063
Tachigali	*Versicolor*	Fabaceae	Rem	OC	0.709	0.070
Cordia	*Bicolor*	Boraginaceae	Ref	OC	0.823	0.103
Ficus	*Insipida*	Moraceae	Ref	OC	0.743	0.143
Ficus	*Insipida*	Moraceae	Ref	OC	0.495	0.093
Hieronyma	*Alchorneoides*	Euphorbiaceae	Ref	OC	0.746	0.091
Hieronyma	*Alchorneoides*	Euphorbiaceae	Ref	LR	0.596	0.064
Inga	*Multijuga*	Fabaceae	Ref	OC	0.579	0.083
Spondias	*Mombin*	Anacardiaceae	Ref	OC	0.524	0.061
Virola	*Sebifera*	Myristicaceae	Ref	LR	0.752	0.030
Vochysia	*Ferruginea*	Vochysiaceae	Ref	LR	0.651	0.078
Vochysia	*Ferruginea*	Vochysiaceae	Ref	LR	0.618	0.053

Table 4. The top ten species found around each type of tree based around the Importance Value Index (IVI – listed). IVI totals to 300 for each type of focal tree; all species listed account for about half (less for remnant trees) of the total IVI.

	Reference Species	**IVI**	**Remnant Species**	**IVI**
1	*Apeiba tibourbou* (Tiliaceae)	34.87114	*Socratea exorrhiza* (Arecaceae)	16.94607
2	*Spondias mombin* (Anacardiaceae)	21.87522	*Chimarrhis latifolia* (Rubiaceae)	16.236
3	*Luehea seemannii* (Tiliaceae)	19.99436	*Apeiba tibourbou* (Tiliaceae)	15.54992
4	*Piper sp.* (Piperaceae)	11.58067	*Castilla tunu* (Fabaceae)	14.34716
5	*Cordia bicolor* (Boraginaceae)	11.2924	*Ficus insipida* (Moraceae)	13.20925
6	*Lacistema aggregatum* (Flacourtiaceae)	10.91438	*Piper sp.* (Piperaceae)	11.75848
7	*Castilla tunu* (Moraceae)	10.2199	*Spondias mombin* (Anacardiaceae)	11.53323
8	*Goethalsia meiantha* (Tiliaceae)	8.845922	*Alchornea costaricensis* (Euphorbiaceae)	11.31427
9	*Simaba cedron* (Simaroubaceae)	8.437549	*Goethalsia meiantha* (Tiliaceae)	11.15088
10	*Vochysia ferruginea* (Vochysiaceae)	7.75671	*Tetrathylacium macrophyllum* (Flacourtiaceae)	10.85843
	Total	**145.7882**	**Total**	**132.9037**

Table 5. Calculated alpha and beta diversity for remnant and reference trees for Hill numbers 0 (species richness), 1 (Shannon exponential diversity), and 2 (inverse Simpson diversity).

Hill number	Remnant alpha diversity	Reference alpha diversity	Remnant beta diversity	Reference beta diversity
0	26.90	21.27	4.275	4.481
1	18.60	14.68	3.021	3.145
2	12.09	10.27	2.815	2.872

Table 6. Percentage of each type of dispersal around reference and remnant trees based on species abundance. Confidence intervals listed are 95% confidence intervals around the mean. Significance is assessed by whether or not the 95% confidence intervals overlap; no significant differences in the proportions of dispersers between remnant and reference trees were found.

	Remnant	Reference
Animal (mean)	81.10%	82.86%
Animal (95% CI)	77.88-84.14%	80.59-83.63%
Explosive (mean)	4.52%	1.43%
Explosive (95% CI)	3.007-6.322%	0.820-1.651%
Gravity (mean)	0.50%	1.16%
Gravity (95% CI)	0.103-1.204%	0.621-1.359%
Wind (mean)	13.88%	14.55%
Wind (95% CI)	11.23-16.77%	12.55-15.25%

Table 7. Species classified as OG Specialist, SG Specialist, or Generalist from the chronosequence survey that were also found in our survey quadrats.

OG Specialist Species	**SG Specialist Species**	**Generalist Species**
Cheiloclinium cognatum	*Apeiba tibourbou*	*Anaxagorea crassipetala*
Dialium guianense	*Callicarpa acuminata*	*Brosimum guianense*
Guarea williamsii	*Cordia bicolor*	*Brosimum lactescens*
Gustavia brachycarpa	*Croton schiedeanus*	*Brosimum utile*
Licaria misanthlae	*Cupania rufescens*	*Carapa nicaraguensis*
Pourouma bicolor	*Ficus insipida*	*Castilla tunu*
Protium ravenii	*Goethalsia meiantha*	*Chimarrhis latifolia*
Pseudolmedia spuria	*Guazuma ulmifolia*	*Garcinia madruno*
Socratea exorrhiza	*Hyeronima alchorneoides*	*Guatteria amplifolia*
Tetragastris panamensis	*Inga multijuga*	*Inga litoralis*
	Inga thibaurdiana	*Otoba novogranatensis*
	Lacistema aggregatum	*Perebea hispidula*
	Lonchocarpus macrophyllus	*Simaba cedron*
	Luehea seemannii	*Tapirira myriantha*
	Miconia argentea	*Tetrathylacium macrophyllum*
	Palicourea guianensis	*Vantanea barbouri*
	Siparuna gesnerioides	*Virola koschnyi*
	Spondias mombin	*Virola sebifera*
	Trichospermum galeotti	
	Vochysia ferruginea	

Table 8. Proportion of individuals of each classification type found around remnant (Rem) and reference (Ref) trees. Confidence intervals listed are 95% confidence intervals around the mean. Stars next to means indicates a significant difference between the proportion of individuals of that classification type around remnant trees and around reference trees. Significance was assessed by whether or not the 95% confidence intervals around the mean overlapped.

	≥5 cm dbh				≥10 cm dbh			
	Rem mean	**Rem 95% CI**	**Ref mean**	**Ref 95% CI**	**Rem mean**	**Rem 95% CI**	**Ref mean**	**Ref 95% CI**
OG Specialist	15.79*	12.88-18.91	5.42*	4.14-6.86	16.28*	12.04-21.05	3.8*	2.35-5.60
SG Specialist	27.58*	23.91-31.36	46.67*	43.65-49.69	31.78*	26.22-37.60	56.27*	52.01-60.46
Generalist	28.87*	25.16-32.71	22.19*	19.74-24.76	22.47	17.57-27.76	15.40	12.45-18.6
Rare	27.76	24.08-31.60	25.72	23.12-28.40	29.46	24.04-35.15	24.53	20.96-28.28

Figures

Figure 1. (a) Remnant trees (black dots within white ring), and reference trees (white dots) on Osa Conservation land. The aerial photograph was taken in 1976. The white line indicates the boundary of old growth forest at greatest known level of clearing (not necessarily 1976). The image was processed in ArcMap 9.3.1. (b) Remnant trees (black dots within white ring) and reference trees (white dots) on Lapa Ríos Ecolodge and Wildlife Reserve land. The aerial photograph was taken in 1976. The white line indicates the boundary of old growth forest at greatest known level of clearing (not necessarily 1976). The image was processed in ArcMap 9.3.1. (c) Remnant trees (dark grey flags) and reference trees (white flags) on Osa Conservation land. Satellite imagery is from 2009 and copyright Google Earth and GeoEye. (d) Remnant trees (dark grey flags) and reference trees (white flags) on Lapa Ríos Ecolodge and Wildlife Reserve land. Satellite imagery is from 2009 and copyright Google Earth and GeoEye.

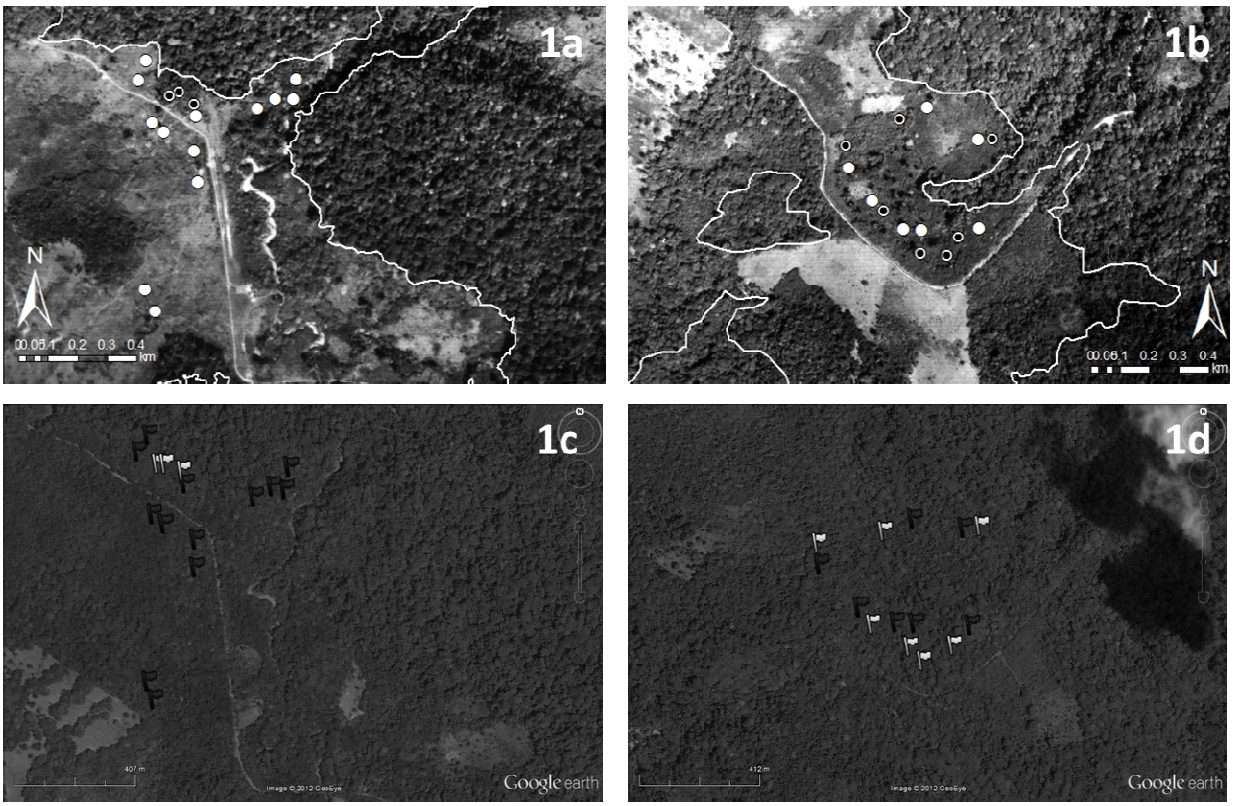


Figure 2. a) Species accumulation curves for the forest around remnant and reference trees, for all stems ≥5 cm dbh. All species accumulation curves are extrapolated to 76 individuals, the greatest number of individuals found in one plot. The fewest number of individuals in a single plot is 30; the average number of individuals in a single plot is 53.6. b) Species accumulation curves for the forest around remnant and reference trees, for all stems ≥10 cm dbh. All species accumulation curves are extrapolated to 40 individuals, the greatest number of individuals found in one plot. The fewest number of individuals in a single plot is 13; the average number of individuals in a single plot is 25.9.

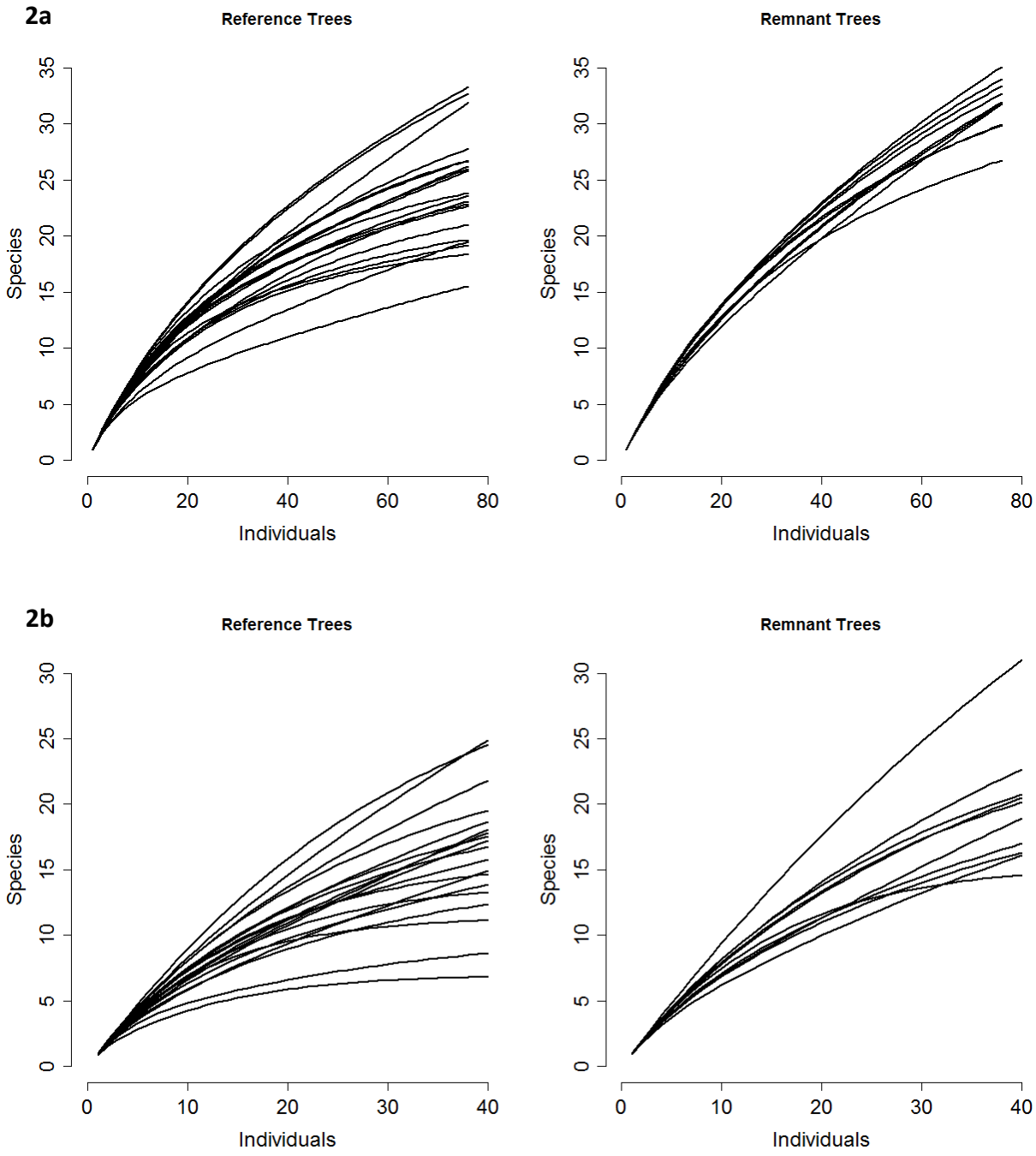


Figure 3. a) Species composition around all trees, plotted in NMDS space and grouped by focal tree type. For forest composition around remnant trees or references trees, central tree was not included in the analysis. Convex hulls are drawn as the shortest distance between all of the outermost points to encapsulate all of the points in NMDS space for one type of focal tree (reference or remnant). b) Species composition around all trees, plotted in NMDS space and grouped by focal tree type, for stems ≥10 cm dbh. Convex hulls are drawn as the shortest distance between all of the outermost points to encapsulate all of the points in NMDS space for one type of focal tree (reference or remnant).

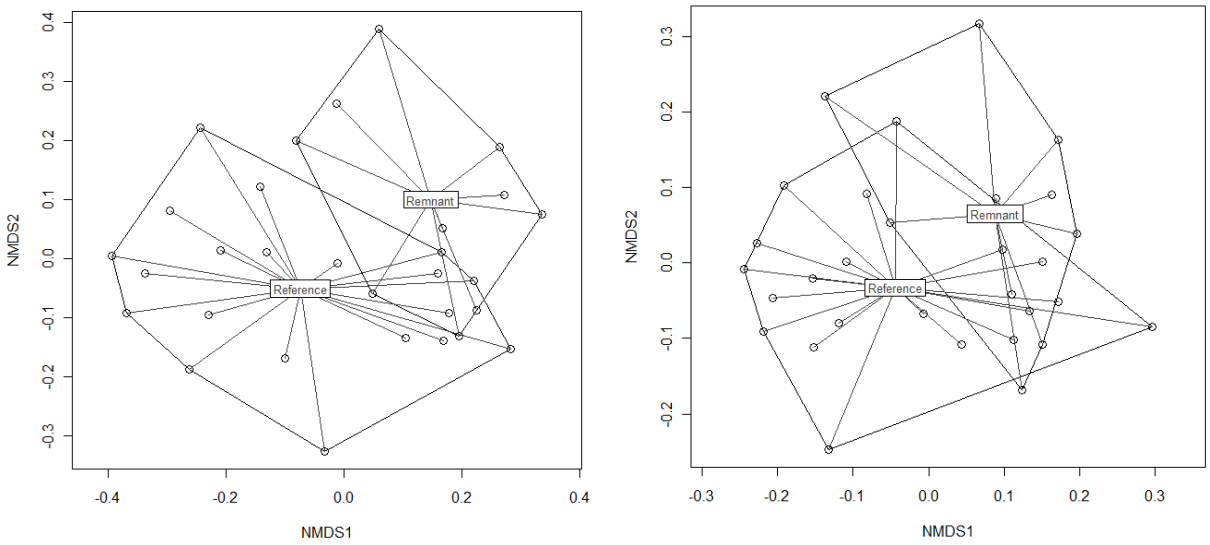


Figure 4. The species composition of all early second growth and old growth forest at the two surveyed sites, plotted in NMDS space. For forest composition around remnant trees or references trees, central tree was not included in the analysis. Convex hulls are drawn as the shortest distance between all of the outermost points to encapsulate all of the points in NMDS space for one type of forest (5-15 years since pasture abandonment (5-15_LR), 15-30 years since pasture abandonment (15-30_LR or 15-30_OC), reference forest (Ref_LR or Ref_OC), remnant forest (Rem_LR or Rem_OC), and old growth forest (200_LR or 200_OC)).
Note the progression of age of forest from left (youngest) to right (oldest). NMDS axis 1 separates by similarity to old growth forest species composition, and NMDS axis 2 separates by site. All 0.5 ha forest survey sites marked LR or OC were near but not always on Lapa Ríos or Osa Conservation land.

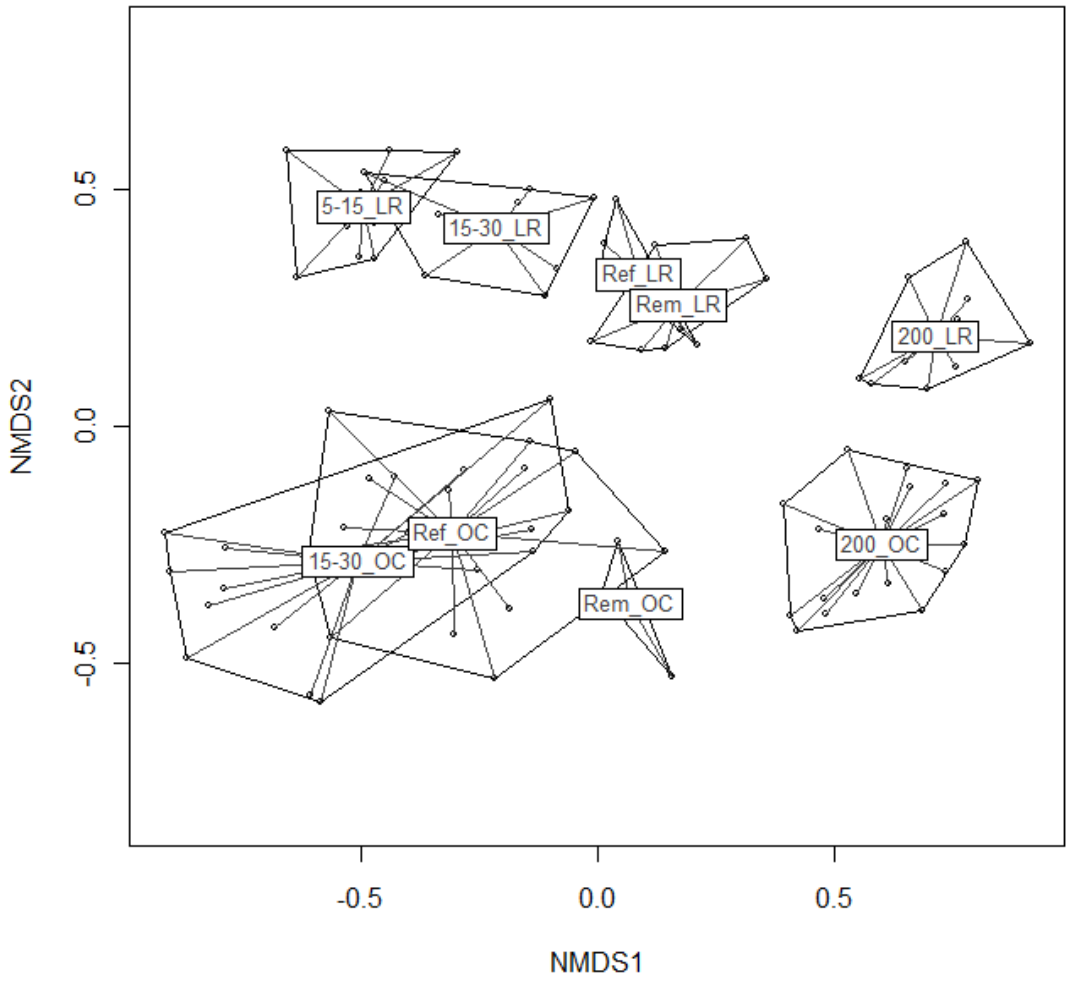


Figure 5. Pairwise similarities between forest around reference trees (on right, “Ref”) and nearby old growth forest and forest around remnant trees (on left, “Rem”) and nearby old growth forest. The Chao-Jaccard Estimated Abundance index returns no similarity in species composition as 0 and complete similarity in species composition as 1. Pairwise similarity was square-root-transformed to make the distributions closer to normal. The central line of the box plot represents the mean of pairwise similarities between reference forest and nearby old growth forest (Ref) or between remnant forest (Rem) and nearby old growth forest. The lower and upper lines of the boxplot represent the 25th percentile and 75th percentile, respectively, for that group.

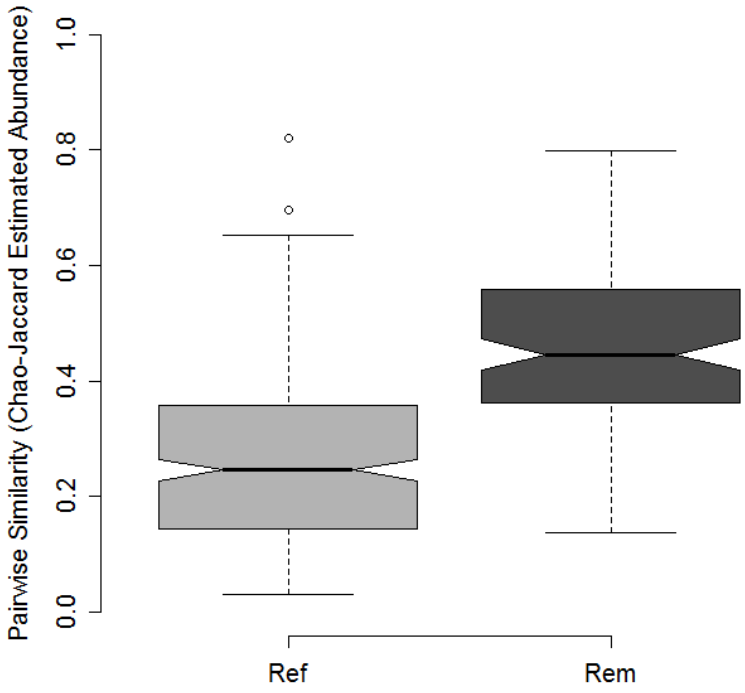
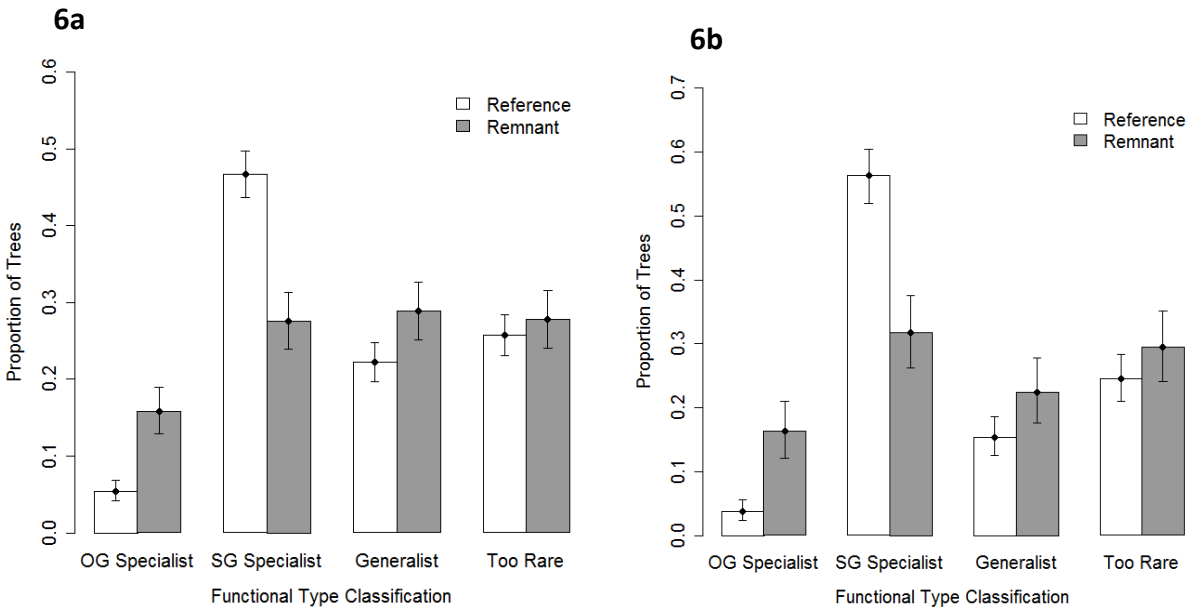


Figure 6. a) Relative proportions of each classification type found around reference and remnant trees. Proportions are such that all four categories for one focal tree type sum to 1. Statistical significance was assessed by whether or not the Bayesian posterior 95% confidence intervals of the proportions overlapped between remnant and reference forest. b) Relative proportions of each classification type found around reference and remnant trees, for stems ≥10 cm dbh. Statistical significance was assessed by whether or not the Bayesian posterior 95% confidence intervals of the proportions overlapped between remnant and reference forest.



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Appendix

Appendix 1. All identified species found in all plots with dispersal mechanism. Dispersal mechanisms with "(G)" means that no information for that specific species was found and genus level information was used; "(F)" denotes that no information for that genus or species was found and family level information was used. References are for dispersal mechanism. "STRI" denotes STRI Herbarium (http://biogeodb.stri.si.edu/herbarium/). All families are according to STRI Herbarium.

Family	**Species**	**Dispersal Mech.**	**Reference**
Anacardiaceae	*Anacardium excelsum*	Animal	Chazdon *et al.* 2003
Anacardiaceae	*Spondias mombin*	Animal	Chazdon *et al.* 2003
Anacardiaceae	*Spondias radlkoferi*	Animal	Chazdon *et al.* 2003
Anacardiaceae	*Tapirira guianensis*	Animal	Berreto *et al.* 2011
Anacardiaceae	*Tapirira myriantha*	Animal	Chazdon *et al.* 2003
Annonaceae	*Guatteria amplifolia*	Animal	STRI
Annonaceae	*Guatteria rostrata*	animal (G)	Harmon 2004
Annonaceae	*Oxandra venezuelana*	animal (G)	Foster and Janson 1985
Annonaceae	*Anaxagorea crassipetala*	explosive	Chazdon *et al.* 2003
Apocynaceae	*Lacmellea panamensis*	Animal	Chazdon *et al.* 2003
Apocynaceae	*Stemmadenia donnell-smithii*	Animal	Chazdon *et al.* 2003
Apocynaceae	*Aspidosperma spruceanum*	Wind	Chazdon *et al.* 2003
Araliaceae	*Dendropanax arboreus*	Animal	Chazdon *et al.* 2003
Arecaceae	*Astrocarium standleyanum*	Animal	Chazdon *et al.* 2003
Arecaceae	*Attalea butyracea*	Animal	Chazdon *et al.* 2003
Arecaceae	*Socratea exorrhiza*	Animal	Chazdon *et al.* 2003
Arecaceae	*Bactris baileyana*	animal (G)	Haber *et al.* 2000
Bignoniaceae	*Crescentia cujete*	animal, water	Gargiullo *et al.* 2008
Bignoniaceae	*Tabebuia chrysantha*	Wind	Jara-Guerrero *et al.* 2011
Bignoniaceae	*Tabebuia rosea*	Wind	STRI
Bombacaceae	*Quararibea asterolepis*	Animal	STRI
Bombacaceae	*Ochroma pyramidale*	Wind	Chazdon *et al.* 2003
Boraginaceae	*Cordia bicolor*	Animal	Chazdon *et al.* 2003
Burseraceae	*Bursera simaruba*	Animal	Chazdon *et al.* 2003
Burseraceae	*Protium confusum*	Animal	STRI
Burseraceae	*Protium copal*	Animal	Murray *et al.* 2008
Burseraceae	*Protium ravenii*	Animal	Murray *et al.* 2008
Burseraceae	*Protium schipii*	Animal	Murray *et al.* 2008
Burseraceae	*Tetragastris panamensis*	Gravity	Chazdon *et al.* 2003
Cannabaceae	*Celtis schippi*	Animal	Chazdon *et al.* 2003

Caryocaraceae	*Caryocar costarricenses*	Animal	Jimenez *et al.* 2002
Cecropiaceae	*Pourouma bicolor*	Animal	Chazdon *et al.* 2003
Chrysobalanaceae	*Hirtella sp.*	animal (G)	STRI
Clusiaceae	*Calophyllum brasiliense*	Animal	Chazdon *et al.* 2003
Clusiaceae	*Garcinia madruno*	Animal	STRI
Clusiaceae	*Symphonia globulifera*	Animal	Chazdon *et al.* 2003
Clusiaceae	*Vismia baccifera*	Animal	Chazdon *et al.* 2003
Clusiaceae	*Tovomita glauca*	animal (G)	STRI
Combretaceae	*Terminalia Amazonia*	Wind	Chazdon *et al.* 2003
Eleaocarpaceae	*Sloanea picapica*	Animal	Harmon 2004
Euphorbiaceae	*Alchornea costaricensis*	Animal	Chazdon *et al.* 2003
Euphorbiaceae	*Alchornea latifolia*	Animal	Chazdon *et al.* 2003
Euphorbiaceae	*Hyeronima alchorneoides*	Animal	Chazdon *et al.* 2003
Euphorbiaceae	*Sapium laurifolium*	animal (G)	Haber *et al.* 2000
Euphorbiaceae	*Croton schiedeanus*	explosive	Chazdon *et al.* 2003
Fabaceae	*Dialium guianense*	Animal	STRI
Fabaceae	*Inga multijuga*	Animal	STRI
Fabaceae	*Inga nobilis*	Animal	STRI
Fabaceae	*Inga oerstediana*	Animal	Chazdon *et al.* 2003
Fabaceae	*Inga sapindoides*	Animal	Chazdon *et al.* 2003
Fabaceae	*Inga thibaurdiana*	Animal	Chazdon *et al.* 2003
Fabaceae	*Ormosia macrocalyx*	Animal	Chazdon *et al.* 2003
Fabaceae	*Swartzia simplex*	Animal	Chazdon *et al.* 2003
Fabaceae	*Erythrina sp.*	animal (G)	STRI
Fabaceae	*Inga acrocephala*	animal (G)	STRI
Fabaceae	*Inga alba*	animal (G)	STRI
Fabaceae	*Inga bella*	animal (G)	STRI
Fabaceae	*Inga litoralis*	animal (G)	STRI
Fabaceae	*Inga venusta*	animal (G)	STRI
Fabaceae	*Ormosia coccinea*	animal, gravity	Harmon 2004
Fabaceae	*Diphysa Americana*	Wind	Jimenez *et al.* 2002
Fabaceae	*Lonchocarpus (heptophilus or pentophilus)*	Wind	Chazdon *et al.* 2003
Fabaceae	*Tachigali versicolor*	Wind	STRI
Fabaceae	*Pterocarpus violaceus*	wind (G)	Chazdon *et al.* 2003; Jara-Guerrero *et al.* 2011
Fabaceae	*Lonchocarpus macrophyllus*	wind or explosive	Chazdon *et al.* 2003; Jara-Guerrero *et al.* 2011; Murray *et al.* 2008
Flacourtiaceae	*Lacistema aggregatum*	Animal	Chazdon *et al.* 2003
Flacourtiaceae	*Laetia procera*	Animal	Chazdon *et al.* 2003

Flacourtiaceae	*Lozania pittieri*	Animal	STRI
Flacourtiaceae	*Mayna odorata*	Animal	Foster and Janson 1985
Flacourtiaceae	*Xylosma intermedia*	Animal	Harmon 2004
Flacourtiaceae	*Tetrathylacium macrophyllum*	animal (G)	Harmon 2004
Hippocrataceae	*Cheiloclinium cognatum/Salacia cognate*	animal (G)	Haber *et al.* 2000
Humiriaceae	*Vantanea barbourii*	Animal	Jimenez *et al.* 2002
Lamiaceae	*Callicarpa acuminate*	Animal	Chazdon *et al.* 2003
Lauraceae	*Nectandra umbrosa*	Animal	STRI
Lauraceae	*Ocotea cernua*	Animal	Chazdon *et al.* 2003
Lauraceae	*Licaria misanthlae*	animal (F)	Haber *et al.* 2000
Lauraceae	*Licaria sp.*	animal (F)	Haber *et al.* 2000
Lauraceae	*Cinnamomum sp.*	animal (G)	Berreto *et al.* 2011
Lauraceae	*Ocotea ira*	animal (G)	Haber *et al.* 2000
Lauraceae	*Ocotea sinuate*	animal (G)	Haber *et al.* 2000
Lauraceae	*Ocotea sp. I*	animal (G)	Haber *et al.* 2000
Lauraceae	*Ocotea sp. II*	animal (G)	Haber *et al.* 2000
Lecythidaceae	*Gustavia brachycarpa*	animal (G)	STRI
Malpighiaceae	*Bunchosia macrophylla*	Animal	Chazdon *et al.* 2003
Malpighiaceae	*Byrsonima crassifolia*	Animal	Chazdon *et al.* 2003
Malpighiaceae	*Byrsonima crispa*	Animal	Chazdon *et al.* 2003
Melastomataceae	*Miconia affinis*	Animal	Chazdon *et al.* 2003
Melastomataceae	*Miconia argentea*	Animal	Chazdon *et al.* 2003
Melastomataceae	*Miconia elata*	Animal	Chazdon *et al.* 2003
Melastomataceae	*Miconia hondurensis*	Animal	Chazdon *et al.* 2003
Melastomataceae	*Miconia multispicata*	Animal	Chazdon *et al.* 2003
Melastomataceae	*Miconia schlimii*	Animal	Harmon 2004
Melastomataceae	*Conostegia icosandra*	animal (G)	Murray *et al.* 2008
Melastomataceae	*Miconia dissitinervia*	animal (G)	Haber *et al.* 2000
Meliaceae	*Guarea bullata*	Animal	Chazdon *et al.* 2003
Meliaceae	*Guarea grandifolia*	Animal	Chazdon *et al.* 2003
Meliaceae	*Guarea chiricana*	animal (G)	Murray *et al.* 2008
Meliaceae	*Guarea williamsii*	animal (G)	Murray *et al.* 2008
Meliaceae	*Carapa nicaraguensis*	animal, water	Chazdon *et al.* 2003
Meliaceae	*Cedrela odorata*	Wind	Jara-Guerrero *et al.* 2011
Moraceae	*Brosimum alicastrum*	Animal	Chazdon *et al.* 2003
Moraceae	*Brosimum guianense*	Animal	Chazdon *et al.* 2003
Moraceae	*Brosimum lactescens*	Animal	Chazdon *et al.* 2003
Moraceae	*Brosimum utile*	Animal	Chazdon *et al.* 2003
Moraceae	*Ficus insipida*	Animal	STRI

Moraceae	*Ficus maxima*	Animal	Jara-Guerrero *et al.* 2011
Moraceae	*Maquira costaricana*	Animal	Chazdon *et al.* 2003
Moraceae	*Pseudolmedia spuria*	Animal	STRI
Moraceae	*Sorocea pubivena*	Animal	Chazdon *et al.* 2003
Moraceae	*Trophis racemosa*	Animal	Chazdon *et al.* 2003
Moraceae	*Castilla tunu*	animal (G)	Haber *et al.* 2000
Moraceae	*Ficus sarsalensis*	animal (G)	Murray *et al.* 2008
Moraceae	*Perebea hispidula*	animal (G)	STRI
Myristicaceae	*Virola koschnyi*	Animal	Chazdon *et al.* 2003
Myristicaceae	*Virola sebifera*	Animal	Chazdon *et al.* 2003
Myristicaceae	*Virola surinamensis*	Animal	STRI
Myristicaceae	*Virola macrantha*	animal (G)	Jimenez *et al.* 2002
Myristicaceae	*Virola macrocarpa*	animal (G)	Jimenez *et al.* 2002
Myristicaceae	*Virola sp. a*	animal (G)	Jimenez *et al.* 2002
Myristicaceae	*Otoba novogranatensis*	animal, water	Chazdon *et al.* 2003
Myrtaceae	*Myrcia splendens*	Animal	Berreto *et al.* 2011
Myrtaceae	*Psidium guajava*	Animal	Jara-Guerrero *et al.* 2011
Nyctaginaceae	*Neea psychotroides*	Animal	Chazdon *et al.* 2003
Olacaceae	*Heisteria acuminate*	Animal	STRI
Olacaceae	*Heisteria concinna*	Animal	Chazdon *et al.* 2003
Oleaceae	*Chionanthus panamensis*	Animal	Haber *et al.* 2000
Piperaceae	*Piper sp.*	Animal	Chazdon *et al.* 2003
Polygonaceae	*Coccoloba tuerckheimii*	Animal	Chazdon *et al.* 2003
Polygonaceae	*Coccoloba sp.*	animal (G)	Jara-Guerrero *et al.* 2011
Rubiaceae	*Borojoa patinoi*	Animal	Chazdon *et al.* 2003
Rubiaceae	*Chomelia microloba*	Animal	Harmon 2004
Rubiaceae	*Faramea occidentalis*	Animal	STRI
Rubiaceae	*Genipa Americana*	Animal	STRI
Rubiaceae	*Guettarda foliacea*	Animal	STRI
Rubiaceae	*Isertia laevis*	Animal	Guenter *et al.* 2008
Rubiaceae	*Palicourea guianensis*	Animal	STRI
Rubiaceae	*Psychotria grandis*	Animal	Chazdon *et al.* 2003
Rubiaceae	*Randia sp.*	Animal	Jara-Guerrero *et al.* 2011
Rubiaceae	*Chomelia tenuiflora*	animal (G)	Harmon 2004
Rubiaceae	*Guettarda macrosperma*	animal (G)	Murray *et al.* 2008
Rubiaceae	*Guettarda turrialbana*	animal (G)	Murray *et al.* 2008
Rubiaceae	*Hamelia magnifolia*	animal (G)	STRI
Rubiaceae	*Pentagonia tinajita*	animal (G)	STRI
Rubiaceae	*Psychotria solitudinum*	animal (G)	STRI
Rubiaceae	*Chimarrhis latifolia*	Wind	Harmon 2004

Rubiaceae	*Chione sylvicola*	Animal	Murray *et al.* 2008
Rutaceae	*Zanthoxylum panamense*	Animal	Chazdon *et al.* 2003
Rutaceae	*Citrus limonia*	animal (G)	Haber *et al.* 2000
Saliaceae	*Casearia commersoniana*	Animal	Chazdon *et al.* 2003
Saliaceae	*Casearia corymbosa*	Animal	Chazdon *et al.* 2003
Saliaceae	*Casearia sylvestris*	Animal	Chazdon *et al.* 2003
Sapindaceae	*Cupania rufescens*	Animal	Chazdon *et al.* 2003
Sapindaceae	*Talisia nervosa*	Animal	Chazdon *et al.* 2003
Sapotaceae	*Pouteria chiricana*	Animal	Murray *et al.* 2008
Sapotaceae	*Pouteria torta*	Animal	Chazdon *et al.* 2003
Simaroubaceae	*Simarouba amara*	Animal	Chazdon *et al.* 2003
Simaroubaceae	*Simaba cedron*	animal, water	Waring and Running 2007
Siparunaceae	*Siparuna gesnerioides*	Animal	Harmon 2004
Siparunaceae	*Siparuna sp.*	animal (G)	Jara-Guerrero *et al.* 2011
Solanaceae	*Cestrum schlectendahlii*	animal (G)	Haber *et al.* 2000
Sterculiaceae	*Guazuma ulmifolia*	Animal	Jara-Guerrero *et al.* 2011
Sterculiaceae	*Sterculia apetala*	Animal	STRI
Tiliaceae	*Apeiba tibourbou*	Animal	Chazdon *et al.* 2003
Tiliaceae	*Goethalsia meiantha*	Wind	Chazdon *et al.* 2003
Tiliaceae	*Luehea seemannii*	Wind	Chazdon *et al.* 2003
Tiliaceae	*Trichospermum galeotti*	Wind	Chazdon *et al.* 2003
Turneraceae	*Erblichia odorata*	wind?	
Urticaceae	*Cecropia insignis*	Animal	Chazdon *et al.* 2003
Urticaceae	*Cecropia obtusifolia*	Animal	Chazdon *et al.* 2003
Verbenaceae	*Aegiphila panamensis*	Animal	Chazdon *et al.* 2003
Verbenaceae	*Vitex cooperi*	Animal	Chazdon *et al.* 2003
Vochysiaceae	*Vochysia ferruginea*	Wind	Chazdon *et al.* 2003
Vochysiaceae	*Vochysia guatemalensis*	Wind	Chazdon *et al.* 2003